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NOTES ON THE CALIFORNIAN SPECIES OF *TRILLIUM* L.

I. A REPORT OF THE GENERAL RESULTS OF FIELD AND GARDEN STUDIES, 1911–1916

BY

THOMAS HARPER GOODSPEED AND ROBERT PERCY BRANDT

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For the past six years a study of the species of *Trillium* peculiar especially to Western Middle California has been carried on under the general supervision of the senior author with a number of assistants. The investigation was originally undertaken at the suggestion of Professor W. L. Jepson, who pointed out the remarkable range of color variation in *Trillium sessile* var. *giganteum* H. & A. and suggested that it might be possible to segregate color forms geographically. It was also suggested that garden studies might throw light upon their origin. Interest at the start thus centered about the range and origin of color variation in *T. sessile* var. *giganteum;* the extent of the investigation necessary in this connection has brought up a large number of problems seemingly of equal or greater interest. Indeed, it has been found necessary to extend the investigation to include comparative studies of *T. ovatum* Pursh. The present report aims to treat very briefly of the systematic position of the various species of *Trillium* native to California and to include a description of the general results of field and garden studies primarily upon *T. sessile* var. *giganteum.*

Field studies of var. *giganteum* have covered rather thoroughly the territory which is fairly definitely limited by the term Western Middle California.[1] That portion of the Coast Range which borders upon San Francisco Bay on the east and may be spoken of as the

[1] Jepson, W. L., Flora of Western Middle California, San Francisco, 1911.

Berkeley and Oakland Hills has, by reason of its accessibility, received principal attention. Extensive studies have, however, been carried on to the north in Napa Valley (Napa County), in Southern Mendocino County and in Marin County. To the south certain stations in Monterey County, Santa Cruz County and San Mateo County have received attention and rather thorough study. Our own field studies have from time to time been supplemented by examination of plants sent in by a considerable number of correspondents. Collections by the latter have added Sonoma County to the above list and have furnished valuable comparative material from stations in the same general regions from which our own collections have come. Beyond the range indicated above, some study has been made at stations near Dutch Flat, Placer County (3500 ft.) and at Crockers, Tuolumne County (4500 ft.).

Two seasons, a dry and a wet season, comprise the range of climatic conditions peculiar to that portion of California with which we here are dealing. In general the month of January, which includes the period of greatest precipitation, is the coldest, whereas during August, the driest month, highest temperature conditions usually prevail. The two tables below, Table 1 for San Francisco and Table 2 for Berkeley, give the approximate average rainfall in inches month by month in the region surrounding San Francisco Bay. As may

Table 1

Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
4.89	3.50	3.34	1.64	0.73	0.16	0.02	0.02	0.32	1.00	2.55	4.51

Table 2

Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
5.81	4.15	4.95	1.49	1.15	0.22	0.02	0.04	0.57	1.48	2.54	4.20

be noted in the above tables, approximately three-fourths of the annual rainfall occurs in the months from December to March inclusive. The figures for July and August refer to heavy mists and slight July rains, which sometimes occur. Precipitation in practically all cases consists of storms of one to thirty or more days' duration, interspersed with periods of clear, dry weather. Precipitation in spring decreases as the storms become shorter and less severe and the intervening periods of clear weather increase in length. In the northern part of California the rainfall is much heavier than in the central part, and very appreciable precipitation may occur in July. Such conditions are also characteristic of the Sierra Nevada. In Southern

California, on the other hand, the rainy season becomes shorter, and the lessened precipitation consists of a few drenching rains of short duration. In addition to the actual precipitation, sea fogs more or less relieve the drought of summer along the Coast. With the exception of the Sierra Nevada, the state is free from severe cold in winter. Under the heavy forests along the northern coast and even under chapparal in the south, frost rarely occurs.

In the Sierra Nevada and along the northern coast high evergreen forest prevails, with low trees and chapparal on high, dry ridges where the soil is shallow and poor. During heavy summer fogs the trees in the coast forest drip very freely. Much of this water is retained, so that the soil is visibly moist at the surface as late as the first of August. Such plants as can endure shade are found here. *Trillium ovatum* Pursh. is one of these. It grows on flats and on both northerly and southerly slopes wherever the soil is sufficiently moist and fertile. It does not grow in the dry chapparal nor on those hot mountain tops where the trees are tall but widely separated. In recently cleared or burned-over areas this plant grows luxuriantly, sending up two shoots a season from a single rootstock and practically always maturing fruits and viable seeds. It does not multiply in such localities, however, because of the use of the seeds for food by animals and birds and because the seeds which are dropped are unable to germinate on account of the extremely dry condition of the surface soil. Toward the inner boundary of the redwood forest, where the influence of fogs is lessened, the forest tends to retire to northerly slopes. *Trillium ovatum* is found only well within the limits of the forest in such locations. Still farther inland the species disappears, to reappear in the northern Sierras.

In certain localities in the Redwood Belt which are exposed to dry winds or have soil too shallow for large trees, the forest is replaced by grassland and thickets of deciduous shrubs and large herbs. *Trillium sessile* var. *giganteum* is peculiar to such associations. This species may also be found near the edges of groves of redwood but never in the dense shade furnished by a close stand of these trees. It also occurs beyond the limits of shrub formations, but rarely in the drier grassy areas.

In Central California the prevailing formation is grassland on southerly exposures, and deciduous shrubbery on northerly slopes with occasional groups of low-growing deciduous or thick-leaved evergreen trees. Such trees and shrubs also form a fringe along streams. Large

perennial herbs are found covering the ground under these trees and shrubs. *Trillium sessile* var. *giganteum* grows in great abundance in this region, but disappears some eight miles east of San Francisco Bay, reappearing in the middle Sierra Nevada. In addition to the prevailing formations noted above, redwood forest occurs in unusually moist cañons of Central California, such as those on Mount Tamalpais and in San Leandro Cañon. *Trillium ovatum* regularly appears in these localities, sometimes in great abundance, while *T. sessile* var. *giganteum* occurs only on the edges of these groves.

Three species of *Trillium* are with certainty to be distinguished as occurring in California. The total range of all the west coast species extends at least from Washington south to San Luis Obispo County, California. The pedunculate species of California are two—*T. ovatum* Pursh., and *T. nivale* Watson. The latter species is not too well known but is reported as characterized by a short, slender habit, petioled leaves, long pedunculate flowers and in general to be "allied to *T. nivale* Riddell, which it much resembles in habit." This species we have not collected and is not to be dealt with in what follows. *Trillium ovatum* is sometimes referred to as the west coast form of *T. grandiflorum* (Michx.) Salisb., from which, however, it is in fact distinctly set apart. In height *ovatum* ranges from 6 to 30 cm. from the surface of the ground, the height of the great majority of the plants falling between 20 and 26 cm. Where the natural cover has disappeared, as in burned-over areas, the west coast species of *Trillium* are greatly reduced in height but vegetative and floral organs are not diminished as to size. In general, height of plants seems scarcely worthy of notice in this genus where the character can be varied at will. This point is emphasized in the reaction shown by the plants figured in plate 1, figure 2. All the four plants were kept under a shed which was open at one side. The two middle plants were grown near the open side and were fully and on all sides almost equally illuminated, while the two plants at either end were grown toward the back of the shed in greater shade and illuminated from one side only. During the year preceding and in the year following when all were growing under the same conditions their height was closely corresponding. The above is mentioned here not because the observed reaction is other than the one to be anticipated, but because the difference in height and habit of the two groups is out of all proportion to the relatively slight difference in growing conditions. In other words, plants of *Trillium* species appear to be so markedly

affected by variation in illumination that height, general habit and, as can be seen, the presence or absence of a slight petiole, are not to be taken as reliable criteria for species differentiated.

T. ovatum is thoroughly described by Jepson,[2] and only a few points are worthy of special mention. In color of flower this species is characteristically a chalky white and the lack of variation in color is striking in connection with the extreme variability of *T. sessile* var. *giganteum* in this character. After anthesis and while fading the petals become distinctly pigmented to such an extent in many cases that the petals may become deep rose-red as they wither. Herbarium specimens of this and other white-flowered species seem to show a considerable variation as to the presence or absence of this pigmented condition. According to our preliminary observations on this matter, it appears that a plant collected before pollination or fertilization may not exhibit the pigmented condition when dried, but that when collected after pollination or fertilization the color will appear on drying even though not apparent when collected.

Turning now to *T. sessile* var. *giganteum*, there seems to be no doubt that this Californian plant represents at least a very distinct modification of the eastern *T. sessile*. The difference in size between the eastern and western forms is very striking and it may ultimately seem desirable to accept the western form as a distinct species under the name *T. giganteum* (H. & A.) Heller. *T. sessile* var. *giganteum* is, again, fully described by Jepson,[3] but a number of points, especially with reference to its variability in certain characters, are worthy of note. Characteristic individuals of the Californian variety of *T. sessile* just coming into full flower are shown in plate 1, figure 1, and in plate 3, figure 6, a vigorous and characteristic plant fully in flower. The very considerable size of all characters may be seen by reference to plates 1 to 3. As noted below, we have undertaken a rather extensive statistical study of the size relations of vegetative and floral characters and it is hoped that measurements of the eastern *T. sessile* can also be obtained. Since our data are not entirely complete and we do not know the exact limits of variation of corresponding characters peculiar to eastern species, it seems best to discuss only in very general fashion the variation in size of the leaves and flower parts of *T. sessile* var. *giganteum*.

At the start it might be noted that for all characters the limits

[2] *Op. cit.*, p. 108.

[3] *Op. cit.*, p. 109; cf. Garden and Forest, vol. 3, p. 320, 1890.

of size variation of the eastern and western forms of *T. sessile* probably overlap slightly, but also that the average individual of the eastern form is throughout strikingly diminutive as compared with its Californian variety. Thus, with reference to length of petal, a very small percentage of the more than five hundred flowers measured have fallen below 4 cm., while 6 to 7 cm. represents perhaps the average length and many measurements show a length of over 8 cm. The relatively few specimens of the eastern *sessile* examined give 4 cm. as the maximum and 1.3 cm. as the minimum length of petal. One other size difference might be mentioned, i.e., leaf size. According to our limited observation, the eastern species bears leaves not over 8 cm. long and always longer than broad, while the smallest specimen measured showed leaves only 4.2 cm. in length. Possibly the largest leaf of the western form observed was 17.5 cm. in length and its greatest width was 19.5 cm. An excess of width over length of leaf is not unusual and may even be characteristic of the plants from certain localities. The minimum length of leaf approximates 5 cm. in one specimen. In this matter of leaf size we are referring only to normally flowering plants of mature structure. It may in general be said that *T. sessile* var. *giganteum* exhibits a most remarkable range of variation as to the size of all characters both vegetative and floral. This situation is illustrated in plate 2, figures 3 and 4, and is sufficiently striking to make unnecessary further comment here. Variations in form and shape of corresponding characters are brought out in these same plates. With reference to this matter of form and shape variation we again prefer to postpone the presentation of the complete data until it may be possible to consider together in full the relation of size, shape and color forms peculiar to definite localities. That the range of variation in shape and form of vegetative and floral organs is as great as their size differences should be sufficiently apparent from the specimens shown in plates 3 and 4. An extreme variation with respect to width of petal is the (*T. sessile*) variety *angustipetalum* of Torrey. This extremely narrow-petalled form represents simply a point in the very wide range of variation in petal width peculiar to the species in California, although it may, as reported, be characteristic of certain definite localities—i.e., the Sierra Nevada—though on plants growing at 3500 feet near Dutch Flat, Placer County, the petals were rather broadly ovate.

With reference to the nature of the apparent gigantism of *T. sessile* var. *giganteum* we have some more or less fragmentary cyto-

logical data. At the suggestion of Professor R. Ruggles Gates we attempted to determine the relative cell size and the relative chromosome number and chromosome size of the eastern and California varieties of *T. sessile* and to make the same comparative studies in the case of *T. grandiflorum* and the rather closely allied *T. ovatum.* This investigation is still in progress, but it appears desirable to mention such results as are at hand. It seems certain that there is no doubling of the chromosome number, as in *Oenothera gigas,* giant races of *Primula sinensis, Spiranthes cernua,* etc., in the California variety of *T. sessile,* nor is there any distinction in chromosome size or constitution between the eastern and Californian varieties of this species. Similarly we have been unable to note any increase of cell size in the Californian as compared with the eastern *T. sessile,* though the measurements made are too few to allow of a definite conclusion in this connection. *Trillium grandiflorum* and *T. ovatum* are not set apart by conspicuous size differences and in cytological details they correspond rather closely one to the other. The chromosome number in *T. sessile* var. *giganteum* was determined by a study of root tips and of the maturation divisions of the microspore mother-cells, while the tentative conclusions as to comparative cell size are based upon measurements of cells of the root tip.

As stated above, the entire investigation in progress dealing with the Californian species of *Trillium* had its origin in an effort to map the distribution of particular color varieties of *T. sessile* var. *giganteum* and to trace their relationships. Our field studies have led us to distinguish three main color types within the Californian form of *sessile.* First, a white-flowered form which is peculiar to the northern portion of our district and which only in isolated cases occurs elsewhere. So far as color of flower is concerned and also with respect to some other characters, this form corresponds to the species described as *Trillium chloropetalum* by Howell. We have studied it most thoroughly in Napa Valley, Napa County. In cañons of the hills on the sides of the valley and in the nearby Napa Range at an altitude of 2000 feet this pigmentless form occurs in rather great abundance. The petals are dull white, somewhat greenish at the bases, and the flower parts within are light green throughout with the exception of the anther coats, which are a light yellow. This form has been sent in from Sonoma, Sonoma County, and apparently occurs also in Lake County. White-flowered individuals only occur near Dutch Flat, Placer County, and may be characteristic of

the Sierras at altitudes of from 3000 to 4500 feet. On Mount St. Helena, however, a peculiarly deep garnet-petalled form is reported and it is very desirable that field studies be made at the head of Napa Valley on the line along which the two color types come into contact. A distinctly white-petalled form is characteristic of Washington, Oregon and of northern California, and Napa Valley appears to represent the southern limit of its range. In the main all the northern white-petalled plants correspond to those in Napa Valley in showing no pigmentation of flower parts, although many plants from southern Mendocino County with pure white petals show evident traces of deep red pigmentation on the stamens and pistil. Isolated individuals which bear flowers entirely colorless have at times been found south of Napa Valley, but they seem best considered as representing a stage in the transition from undeveloped to normal flower which will be discussed in the next paper of this series.

The second distinct color form is one involving variation about a greenish-yellow shade of petal color and is found in the outer Coast Range from Sonoma County south to Monterey County. Plants with green, greenish-yellow, dull orange or reddish-brown petals were first found on Point Reyes peninsula, which is perhaps the northern limit of this color form. It is found predominating in cañons at the base and south of Mount Tamalpais in Marin County and at a number of stations in Santa Cruz County. Within this color form there is a striking absence of white or very light green petalled individuals, though deep garnet flowers are not infrequently found. Among the lighter-colored flowers of this form a brilliant viridine yellow is not an uncommon shade, while in the green-flowered forms the leaves, sepals and petals are indistinguishable so far as color is concerned. In plate 2, figure 3, flowers of Marin County representative of this second color form are shown. The extremes were included for comparison and no attempt was made to indicate the predominance of the lighter color shades. Plate 2, figure 4, from a photograph of dried specimens and included to exhibit size variation, indicates nothing as to the range of color forms to be found in the third color form described below and to which the original plants belonged. Throughout the range of variation in color of this second form, the stamens and pistils uniformly show a greater or lesser amount of pigmentation.

The third color form is in general peculiar to cañons of the hills surrounding San Francisco Bay on the east and southwest—i.e.,

San Francisco County, the western edge of Contra Costa and Alameda counties and northern San Mateo County. The following points seem, in general, to characterize the plants from the region so far as petal color is concerned. First, the strictly pigmentless northern form is not represented; second, the yellow-green color form is not found; and thus, third, every flower is characterized by the presence of red pigmentation on some of its parts. We have here a most remarkable series of color variations, from flowers with petals white to the base but with deep red stamens and pistil to flowers with all the flower parts except anther sacs and stigmatic surfaces of such a deep garnet shade as to appear black (cf. plate 3, figure 6). As has been noted, every significant flower bears some pigmented parts. Delicate rose pink, violet and even bluish shades are common in this color form.

The origin of these three rather sharply distinguishable color forms and their relation to one another is in doubt. The extremely wide variation of the last-mentioned form has suggested original hybridization between the white-flowered northern form and the more heavily pigmented southern forms. There is, however, little doubt that crossing between the plants which at present make up the series does not take place and probably in but very few instances does anything but asexual reproduction increase the number of individuals because of the almost universal occurrence of partial or complete sterility. This wide range of variation in form three may, perhaps, be looked upon as representing normal variation from a pigmented type. Our garden studies of the three color forms give no evidence of variation in color of flowers produced from the same rootstock in different years, and the results of the field studies indicate no variation among the plants vegetatively produced as offsets from a parent rootstock nor variation in color as compared with the parent plant. The complete sterility, indicated by the entire lack of seed production, of the plants in the garden cultures has made it impossible to cross widely separated color forms. We have, as will be noted below, secured seeds of a number of color types of form three which have proved to be viable. There is thus a possibility of obtaining data on the amount of variability of the progeny of a given color form. The three color forms and their varieties taken together may be thought of as the result (1) of an absence of any cell sap pigment or chromatophore color, (2) the presence of anthocyanin derivatives in cell saps of various reactions which may (3) be present in connection with red, orange or yellow chromatophores or (4) green

chloroplast coloration alone. An investigation from this point of view of the nature of the various colors concerned is in progress.

These color forms which seem to be rather strikingly peculiar to certain definite localities might appear superficially to correspond to one another in characters which are of more significance from the point of view of specific differentiation—i.e., size and form characters of vegetative and floral organs. We feel rather certain, however, that more exact quantitative studies will, in some cases at least, reveal correlation between color and other characters, the sum total giving sufficient differentiation from all other forms possibly to indicate specific definition and to warrant specific description. With this in mind we have measured all significant structures whenever collections have been made. The criteria of specific differentiation in the genus *Trillium* are not such that simple size differences of vegetative or floral organs, or even proof that the correlation in size of organs is different in the various color forms, will give convincing evidence on relationships. Such evidence will depend upon demonstration of shape and form differences, and thus it is desirable to find a method according to which the measurements of size of organs can be used in expressing their shape. It is also highly desirable that the tentative use of the combination *T. sessile* var. *giganteum* which later on may seem best changed to *T. giganteum*, both representing efforts to recognize the size distinction between eastern and Californian *sessile* forms, be placed upon a demonstrable basis. It is thus planned to compare the size differences of these geographically distinct *sessile* species, and until this is done we do not propose, as noted above, to present the statistical data at hand.

Rootstocks of *T. sessile* var. *giganteum* were first brought into the University of California Botanical Garden in the spring of 1911. In February, 1916, the total number of rootstocks under observation was nearly 150. We have data on sixty plants over a period of six years and on forty plants over a period of four or five years, while the remainder were introduced into the cultures after 1913. The various localities where, as mentioned above, field studies were made are practically all represented by rootstocks in the Garden. In May, 1914, we secured rootstocks of *T. sessile* L. from New Lennox, Illinois, and rootstocks of *T. grandiflorum* (Michx.) Salisb. from Sawyer, Michigan. During the past two growing seasons we have had a few flowering and a number of flowerless shoots from these rootstocks. From time to time a few rootstocks of *T. ovatum* Pursh. have been

introduced into the cultures, but we have experienced considerable difficulty in keeping them alive.

The rootstocks have, in practically all cases, been grown outdoors in pots. It was impossible even to approximate the soil or environmental conditions from which the different rootstocks had been taken and all were grown in rather light garden soil and under identical cultural conditions. The rootstocks have been repotted yearly, usually in August. The conditions under which the garden cultures have been maintained are the best at our command, but are certainly not the most favorable and may even be the determining cause of certain observed conditions to be described below.

Perhaps the most significant fact concerning the nature of the species of *Trillium* under observation through field and garden studies has to do with the occurrence of undeveloped flowers in those plants which appear to be completely flowerless. This matter is to be taken up separately in the second paper of this series and here it is not necessary to do more than mention the points established. Where a considerable number of *Trillium* plants grow together in a relatively limited area, a glance reveals the fact that some are in flower and that other plants, perhaps by far the larger number, appear to be entirely without flowers, while a few exhibit small, unopened buds in the center of the whorl of leaves. It has, however, been found that every plant contains a flower of a greater or lesser degree of differentiation or development. At one extreme are entirely undifferentiated primordia of microscopic size and at the other are the buds mentioned above which never open and in which the petals are always white and early withering, the pistil suppressed or the ovary lacking ovules, and the anthers without functional pollen. Between these two extremes we have found all intermediate stages. Study of the garden cultures has aided in pointing out the significance of this situation. In only a few instances in the cultures has it been possible to keep the shoots produced from the rootstocks in a normally flowering condition from year to year. Thus, though the great majority of the 150 rootstocks under observation bore a flowering shoot or shoots when collected or during the growing season previous to collection, we have at present scarcely a half dozen rootstocks producing flowering shoots. Usually in the year following collection the shoot or shoots produced contain undeveloped flowers.

Our field studies have in part been concerned with an investigation of the various degrees of sterility exhibited by var. *giganteum*,

a condition in rather striking contrast to that exhibited by *T. ovatum* which almost without exception produces an abundance of seed. In California it is difficult, unless the plants are staked in the spring when in leaf and flower, to find their drying remnants when they are covered with other larger species which have dried down over them. It has, however, been apparent throughout our field and garden studies that many plants of *sessile* do not bear fruit either in a given season or during a number of seasons. Indeed, for some years we did not succeed in finding a single fruit containing seeds, though many plants known to have produced apparently normal flowers were under observation in the field as they ripened down. Further, many other plants examined near the close of their active season above ground were found to mature only a shrunken, undeveloped pistil provided with rudimentary ovules, though these same plants had been strong in appearance and vigorous in growth and at anthesis were provided with pollen and ovules normal in appearance. Again, there are still other plants in the flowers of which at anthesis the pistil is entirely undeveloped. The undeveloped flowers referred to above represent the extreme case of sterility accompanied by the lack of development of all the flower parts. Finally, the almost complete absence of seedlings and young plants, other than those derived vegetatively from older rootstocks, added evidence in support of the contention that lack of seed production was the rule. These earlier observations were confined to stations in the Berkeley hills which by reason of accessibility were favorable for following closely the more obscure periods in the annual life-cycle of the plants. The white-flowered form of var. *giganteum* characteristic of the northern coast counties has more recently been found to seed rather profusely in certain localities or under certain conditions. More recently, also, a number of plants of *sessile* in the Berkeley hills have been found to give viable seed, particularly favorable seasons climatically being perhaps responsible. In general, however, it can be said that *sessile*, in contrast to *ovatum*, is an extremely uncertain producer of seed and that a very considerable number of individuals are not capable of seed production over a course of a number of years.

The fact, as noted above, that plants which apparently produced normal sexual elements failed to form fruit led to an experimental and cytological investigation of the causes of sterility in such cases. In the garden a considerable number of flowers were self-pollinated at different periods before and after anthesis. Cross-pollinations,

also, were made between plants of different flower color and many attempts were made in which pollen of *ovatum* was used on *sessile*. Pollen of *sessile* will give a fairly high percentage of germination in tap water. Still it seemed possible that the erect, open flower of *sessile* borne on a plant which usually grows in open thickets might be subjected to too excessive moisture conditions at pollination and thus flowers in the field and in the garden cultures were protected in various ways during and for a time after pollination. The lack of any positive results following these efforts seems to indicate that moisture conditions are not the determining factors in this connection. It seemed possible that in the rapid growth of the vegetative portions of the shoot the food reserves of the rootstock were depleted sufficiently to make it impossible for the final stages in the maturing of the sex cells to take place normally. With this possibility in mind we cut off one, two, or all three of the leaves when still undeveloped. This treatment was of no value in increasing the amount of normally matured reproductive tissue but, on the other hand, did not appear to interfere with the growth of the stem or the increase in size of the flower bud. The rootstock was, in other cases, cut away from its growing apex at different stages of development of the flower shoot, with the thought that such shock might provide a stimulus to more normal fruiting. In such cases over two-thirds of the rootstock was removed and the plant consisted of nothing but the aerial shoot rising from a small disc of the rootstock. The desired effect was not produced by this treatment but, on the other hand, in only a few cases did the parts of the plant above ground show any effects of the mutilation of parts below ground. Etherization experiments with rootstocks were attempted during the dormant season with the thought that an enforced rest period at this stage might result in the production of more highly fertile flowers. The spores are being matured throughout the dry season when available moisture is at a minimum and it seemed possible that the maturation of the sex cells might be more successfully carried through if the buds in the rootstock crowns were forced to remain inactive until the opening of the wet season. On the other hand, there is, after etherization, often a stimulation to abnormally rapid growth and early development of flowers. A considerable number of rootstocks were treated but no apparent effect in either direction was noted.

As mentioned below, a rootstock may be divided many times and

segments under 5 mm. in thickness will produce shoots and increase in size normally from year to year. We attempted to graft all sizes of rootstock segments of *sessile* onto one another and to unite portions of rootstocks of this species and of *ovatum*. A possible increase in vegetative vigor of the grafted rootstock was anticipated. It was also hoped that, in the case of interspecific graft unions, an offset might be produced at the point of contact. A few successful unions were obtained in both cases, but no visible effects could be noted during the first year in the case of the shoots which were normally produced from the crowns of the treated rootstocks. No offsets were formed during this first year, and the experiments were terminated because it was not possible to give the grafted rootstocks sufficient care to prevent the drying out of the graft unions during the dry season.

Seeds of *T. sessile* var. *giganteum* have from time to time been obtained, both of the white-flowered form of the northern counties and also from plants in the Berkeley hills. Up to this past year it has not been possible to secure germination of any of this seed, although in all cases it appeared to be entirely normally matured. The seed coverings were broken and softened by mechanical means and by the use of sulphuric acid and were subjected to a variety of growing conditions without securing a single germination. Recently seeds from plants growing in the Berkeley hills have germinated over 60 per cent. Apparently seed of the western *sessile* will not germinate for eighteen months or longer if placed in the ground as soon as mature, but if allowed a period of six to twelve months or more for after-ripening will then germinate almost at once when placed under ordinary germinating conditions. The failure of our earlier attempts at germination of this seed was due to a termination of the experiment long before germination could have taken place. Further experiments are in progress to confirm and amplify these preliminary observations. Various stages of development in seedlings of the first year are shown in plate 4. The third and fifth seedling from the left show the seed coats still attached.

Nothing has been more striking throughout our field and garden observations than the extreme development of vegetative propagation in *T. sessile* var. *giganteum*, a condition which appears to be accompanied by or a result of a highly defective power of sexual reproduction. *T. ovatum*, on the other hand, very rarely forms a new

individual asexually and is correspondingly a consistent producer of large numbers of viable seeds. In plate 3, figure 5, is shown the extreme expression of this vegetative method of propagation peculiar to the western *sessile*. Fourteen plants, three of which do not appear in the photograph, were produced by the parent rootstock by lateral budding to form offsets. In the mass of rootstocks shown it was possible to trace in many cases the original connection between the rootstocks, since the older partially decayed portions of the rootstocks were held in position by the heavily matted roots. The difference in the size and thus in the age of the different offsets, the fact that the whole mass was very compact, that the offsets were quite symmetrically arranged about the parent rootstock in the center, the obvious connection between the offsets and the parent and finally the absence of seedlings in the neighborhood seems to leave no room for doubt that this group shown in plate 3, figure 5, is the result solely of asexual reproduction. Further than this we have noted in the field a large number of rootstocks with four to six small, recently produced offsets still attached to the parent and other larger plants nearby which very apparently had been derived from this same parent. The production of small offsets is shown on the rootstock in plate 3, figure 6. The appearance of the plant there illustrated brings up another matter which is of importance in this connection. Just as *T. sessile* var. *giganteum* produces new plants asexually in considerable numbers, so from the "crown," or covering of the growing point, of each rootstock more than one shoot is often sent up annually. In plate 3, figure 6, the parent rootstock is seen to have produced at least five vigorous flowering shoots from buds formed during the dormant season at the bases of the scale-like, sheathing leaves of the crown. *T. ovatum*, on the other hand, rarely sends up more than a single shoot from a rootstock, just as it almost never produces new individuals asexually. The morpohology of the rootstock and especially the structure of the growing apex is to be taken up in detail in a forthcoming paper of this series.

In the garden cultures we have undertaken a study of the nature of the teratological variations which are of such frequent occurrence in the west coast *sessile*. In our cultures three different rootstocks have produced four-leaved shoots in some one given year, the abnormality never having appeared before or thereafter in shoots from the same rootstocks. Fasciated shoots appear, however, in some

cases to be reproduced year after year from the same rootstock, as does the peculiar abnormality which consists of the production of small but fully developed pistils within the placentation of the legitimate ovary. Two cases of pistillody of the perianth, a case in which sepals are reduced to scales, and many cases of petalody of sepals and stamens and duplication of parts have been noted in the field and the rootstocks brought under observation in the garden.

SUMMARY

Following a description of the Californian species of *Trillium*—*T. sessile* var. *giganteum*, *T. ovatum* and *T. nivale*—the following points were brought up and discussed more or less in detail. They represent the results of field and garden studies and in many cases have been mentioned in this first paper of the contemplated series dealing with the Californian species of *Trillium*, simply as preliminary statements of important problems which are being separately attacked in considerable detail.

1. The extent of the size differences between the eastern *T. sessile* L. and its Californian variety *giganteum* H. & A.

2. The wide range of variation in flower color characteristic of the Californian variety of *T. sessile*.

3. The occurrence of a pure white, a yellow-green and a heavily pigmented color form and a definition of their range of distribution.

4. The high degree of sterility exhibited by the Californian *T. sessile* and the lack of any appreciable degree of sterility in *T. ovatum*.

5. The importance of asexual reproduction in *T. sessile* var. *giganteum* and the almost entire absence of the same in *T. ovatum*.

6. The yearly recurrence or lack of recurrence of teratological variations in *T. sessile* var. *giganteum*.

Transmitted April 6, 1916.

PLATE 1

Fig. 1. Two plants of *T. sessile* var. *giganteum* with the soil exposed to show their depth of insertion, the nature of the rootstock, amount of root system and general vigor. The flowers are just on the point of opening.

Fig. 2. Plants from four different rootstocks of *T. sessile* var. *giganteum* to show the effect of reduced and unilateral illumination on height and petiole formation. The two plants in the center were at the front of a shed while the other two plants were three feet back from the open front.

Figure 1

Figure 2

PLATE 2

Fig. 3. Showing the extremes of variation in size and pigmentation of leaves and flower parts. Plants of the yellow-green color form of *T. sessile* var. *giganteum* from Camp Taylor, Marin County.

Fig. 4. Showing variation in size and shape of flower parts in *T. sessile* var. *giganteum*. From herbarium specimens, plants of the Berkeley Hills.

Figure 3

Figure 4

PLATE 3

Fig. 5. Showing possible extent of vegetative reproduction in *T. sessile* var. *giganteum*. Plants from Felton, Santa Cruz County.

Fig. 6. Showing heavily pigmented flower parts, the formation of young offsets and the number of shoots often produced from a single rootstock crown. Plant of *T. sessile* var. *giganteum* from the Berkeley Hills.

Figure 5

Figure 6

PLATE 4

Fig. 7. Seedlings of *T. sessile* var. *giganteum*. Both the third and the last seedling from the left shows the seed coat still attached.

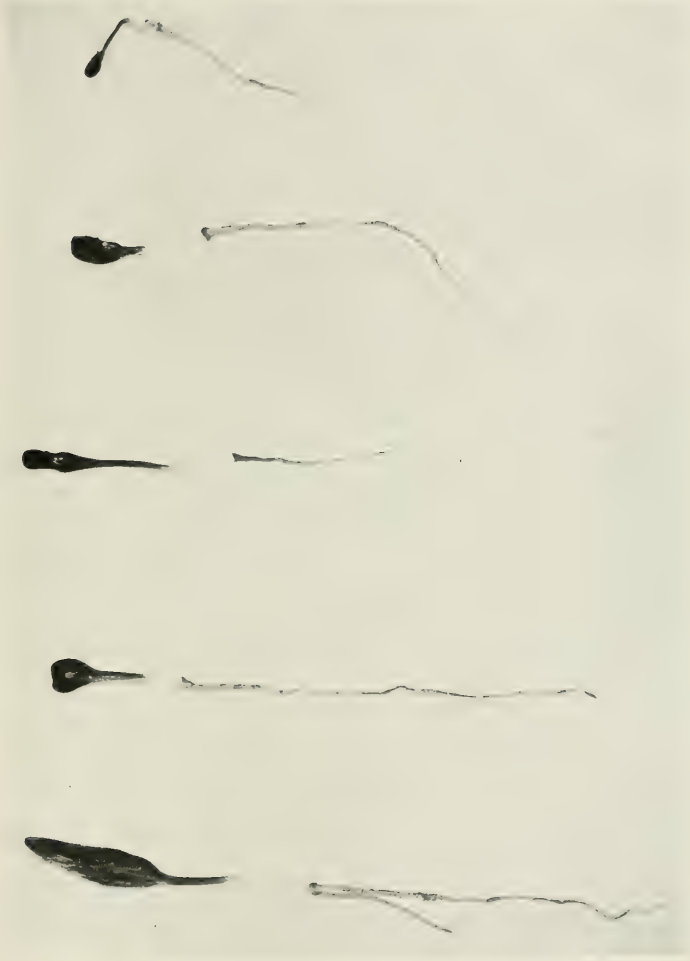

Figure 7

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NOTES ON THE CALIFORNIAN SPECIES OF *TRILLIUM* L.

II. THE NATURE AND OCCURRENCE OF UNDEVELOPED FLOWERS

BY

THOMAS HARPER GOODSPEED AND ROBERT PERCY BRANDT

In the first paper of this series (Goodspeed and Brandt, 1916) reference was made to the fact that when one examines in the field an assemblage apparently of any species of *Trillium*, a considerable number of the plants upon superficial examination appear to contain no floral parts within the whorl of leaves, but upon more careful examination are found to be provided with more or less highly differentiated floral primordia, making up what will be spoken of throughout as "undeveloped" flowers. Plates 5 and 6 show various types of these undeveloped flowers. Table 1, below, consists of measurements of the length of the various structures found in a number of undeveloped flowers of different stages of complexity, the structures measured being named in some cases rather arbitrarily and in general for convenience as though corresponding in position to the distinct floral whorls that make up the normal flower of *Trillium*. From a very large number of specimens examined we are led to make the rather sweeping statement that every plant of *T. sessile* var. *giganteum* H. & A. and *T. ovatum* Pursh., the two species peculiar to Western Middle California, contains floral organs which are either complete in number and differentiation, giving a normal flower, or are reduced in number and differentiation to give various types of undeveloped flowers. In addition, all the apparently flowerless plants of *T. sessile* L. from Illinois and of *T. grandiflorum*

(Michx.) Salisb. from Michigan which we have examined have been found to contain floral rudiments. In addition to the brief report of Smith, noted below, we have been unable to find mention made of these facts, and the present communication is preliminary in the sense that the results of a number of years' investigation herein reported have done little more than point out the lines along which the problem can be attacked. A rather large amount of data based upon observation in the field and upon the results of garden cultures makes it possible to establish certain facts with some definiteness and it thus seems best to submit now the evidence at hand.

Miss A. S. Smith (1896) in collections made on April 5, 1896, near Ithaca, New York, examined fifteen buds, probably still in the rootstock "crowns," which were starting their growth in the partially frozen soil. Only one of the fifteen buds was maturing a normal flower and the remainder apparently corresponded to those figured in plate 6. Miss Smith cut sections in celloidin and reports that

TABLE 1

Length in mm. of the structures making up various sizes of undeveloped flowers in *Trillium sessile* var. *giganteum*

Number	*Sepals*	*Petals*	*Stamens*	*Pistil*
1	24.0	22.0	15.0	8.0
2	23.0	22.0	12.0	7.0
3	22.0	21.0	18.0	8.0
4	22.0	20.0	16.0	7.0
5	18.0	17.0	12.0	7.0
6	16.0	15.0	10.0	7.0
7	12.0	11.0	10.0	5.0
8	11.0	10.0	9.0	6.0
9	10.0	10.0	9.0	3.0
10	9.0	8.0	7.0	3.0
11	8.0	8.0	6.0	3.0
12	7.0	7.0	6.0	1.0
13	3.0	3.0	2.0	1.0
14	2.0	2.0	1.0	0.3
15	1.7	1.6	0.8	0.3
16	1.7	1.2	1.2	0.6
17	0.8	0.6	.....	.....
18	0.6	0.4	.....	.....
19	0.5	0.4	.....	.....
20	0.4	.....	.....	.....
21	0.3	0.1	.....	.....
22	0.2	0.1	.....	.....
23	0.2	.....	.....	.....
24	0.1	0.1	.....	.....
25	0.1	.....	.....	.....

structures representing sepals were often normally matured but within them a "confused mass of cells" occurred. A much larger collection was made in the same region on April 10 of the same year and sixty plants were found to contain "abortive" flower buds, concerning which she says: "Usually the rudiments of a perianth could be distinguished either as a white speck or as very evident floral leaves sometimes 2 to 3 mm. in length, but withered and abortive." Miss Smith suggests that "truly sterile" plants might have been present, but she found none without at least rudimentary floral structures.

The drawings shown in plates 5 and 6 represent median longitudinal sections through the center of the stem apex which in the apparently flowerless shoots is seen as a cuplike depression, on the rim of which the almost completely sessile leaves are borne. The drawings were made from material sectioned in paraffin; while undeveloped flowers of the size shown in plate 6 might be distinguished by the naked eye as minute, white, withered structures in the center of the cuplike depression, those shown in plate 5 would escape notice without magnification. The complete range of variation in size and differentiation of parts given in table 1 is not paralleled in the drawings, wherein only smaller and more rudimentary floral structures are represented. It is important to note in table 1 that a complete series can be obtained, from undeveloped flowers consisting of such minute primordia as these under numbers 17 to 25 to those which are really perfectly matured but functionless buds illustrated under numbers 1 to 3. As mentioned above, we have in this table used the terms petals, sepals, etc., simply for convenience of description in giving the measurements of the structures found. Thus in the case of the smaller group, from numbers 13 to 25, the separation into circles of such structures as are shown in the drawings in plate 5 is a rather arbitrary matter. It must be said, however, that, in dissecting under magnification even these minute organs, one is impressed with the fact that the structures present are arranged in some more or less definite order and inserted at various points upon the reduced receptacle. Certainly in the case of the group of intermediate size, numbers 7 to 12, there is cause for assigning groups of structures to given circles, while in the largest group, numbers 1 to 6, the characteristic floral whorls are perfectly represented. It might also be noted that measurements are at hand which together would form a still more continuous series in which the size of the

structures would vary 0.5 mm. or less between different individuals. The series given in table 1 is sufficiently complete to bring out the points which seem of most significance.

If we turn now to a description of the appearance of these various sizes of undeveloped flowers, the more highly differentiated form—numbers 1 to 6—might first be mentioned. As stated above, these larger undeveloped flowers are really small, fully formed flower buds. They are quite conspicuous, standing in the center of the whorl of leaves, with white, transparent, parchment-like sepals and petals. Such "buds" never open and rapidly dry down as the leaves are fully expanded. The stamens are usually perfect in appearance with anthers fully matured, though they are very slender and perfectly white except along the pollen sacs, which are sometimes a very light yellow in color. Pollen is often present in such cases with every grain shriveled and functionless, while in other cases sporogenous tissue apparently is suppressed entirely in the development of the anthers. The pistil in these largest undeveloped flowers is always functionless and often entirely wanting. Where it does occur the pistil is very much reduced, with diminutive stylar tissue and with no ovules or structures suggesting them in appearance. On *T. ovatum*, a pedunculate species, such large undeveloped flowers at times are to be seen and in these cases a peduncle is present proportional in size to that of the bud. At times, however, this proportion is not maintained, and the small, white bud appears to be sessile, so short is the peduncle upon which it is borne. There is a more or less abrupt transition from the early withering, functionless bud that never opens, although its parts are rather fully and characteristically matured, to the small undeveloped flowers in which all the parts are similar in appearance though differing greatly in size so far as the different circles of perianth segments are concerned. As stated above, the pistil even in the largest undeveloped flowers is often suppressed, the sepals and petals are of the same color, texture and size, and the remainder of the functionless bud consists of narrow, delicate anther-bearing structures. It is in the differentiation of these stamens of more or less characteristic appearance and structure that the rather abrupt transition occurs. Thus all the smaller undeveloped flowers consist of nothing more than minute, white, dry perianth segments which are, in all but those of the smallest size, arranged rather definitely in separate whorls. As shown in plate 5, figure 2, the smallest undeveloped flowers in some cases show a union of the

individual segments to form an enclosed structure which suggests a carpel.

TABLE 2

Production of normal flowering shoots (marked ×) and of shoots with undeveloped flowers (marked –) during six years in garden cultures

Rootstock number	1911	1912	1913	1914	1915	1916	Place of collection
1	×	×	–*	–	–	–	Point Reyes
2	×	×	–	–	–	–	Point Reyes
3	–	–	–	–	–	–	Point Reyes
4	–	–	–	–	–	×	Point Reyes
5	×	–	–	–	–	–	Berkeley Hills
7	×	×	–	–	–	–	Berkeley Hills
9	?	×	–	–	–	–	Berkeley Hills
11	–*	–*	–*	–*	–*	×	Berkeley Hills
29	×	×	–	–	–	–	Berkeley Hills
31	–	–	–	–	–	–	Berkeley Hills
39	×	×	–	–	–	×	Berkeley Hills
45	×	×	×	–	–	–	Point Reyes
48	×	·	–	·	–	–	Berkeley Hills
55	–	–	–	–	–	–	Berkeley Hills
57		–	–	–	–	–	Berkeley Hills
69		×	–	–	–	–	Monterey Peninsula
70		×	–	–	–	–	Monterey Peninsula
71		×	×	×	–	–	Napa Range, 2000 ft.
77		×	–	–	–	–	Crystal Springs, San Mateo Co.
81		×	×	×	–	–	Monterey Peninsula
83		×	×	×	–	–	Monterey Peninsula
88		–	–	–	–	–	Berkeley Hills
93		×	×	×	–	–	Gualala, Mendocino Co.

*Undeveloped flowers of the largest size and most highly differentiated—i.e., buds of almost normal size which never open and wither early.

In connection with an investigation of the nature of these undeveloped flowers we have been concerned with a study of their occurrence both in the field and in garden cultures. As a result we are prepared to make the following general statement: A rootstock bearing a normally flowering shoot in a given year may the following year produce a shoot bearing an undeveloped flower of larger or smaller size, while the reverse sequence of events rarely takes place. This point is emphasized in table 2, in which a cross indicates the production by a rootstock of a shoot or shoots with normal flowers and a dash indicates the presence of an undeveloped flower. A large percentage of the more than 150 rootstocks grown in our garden cultures bore normally flowering shoots when collected, or were known

to have borne such shoots during the season previous to collection. During the present season (1916) only six rootstocks produced such normally flowering shoots and the remainder produced shoots with undeveloped flowers. Table 2 gives the history of twenty-three of the rootstocks in the garden cultures and includes three of the six normally flowering plants of the 1916 season. The other three flowering plants were from rootstocks which have been under observation during two seasons only.

In table 2 characteristic cases were chosen, and a wide range of original habitat of the rootstocks was selected to emphasize the fact that the production of undeveloped flowers is peculiar to all rootstocks, irrespective of the soil or climatic conditions under which they were originally growing. Further, the instances cited include nearly all of the rootstocks which produced normally flowering shoots for more than a single season following collection. Rootstocks 3, 31, 55, 57 and 88 exhibit the extreme condition in that when collected they bore shoots with undeveloped flowers and have continued to produce only such shoots thereafter. Rootstocks 5, 69, 70 and 77 were collected with normally flowering shoots and the following year and thereafter produced shoots with undeveloped flowers only. Rootstocks 1, 2, 7, 29 and 48 and rootstocks 45, 71, 81, 83 and 93 continued to produce normally flowering plants for respectively two and three years following collection and thereafter have produced plants with undeveloped flowers only. There is, then, no doubt that the change from perfectly normal flower to undeveloped flower can take place in a single season and that when this change has once taken place it may, in the majority of cases, be expected to reappear in succeeding years more or less indefinitely. These points have many times been confirmed by field observation during the past six years.

The histories of rootstocks 4, 11 and 39 are obviously of importance in this connection. Here we have cases in which rootstocks have produced only plants with undeveloped flowers for three successive seasons or more and then in a single season have produced plants with large, perfectly normal flowers. In the case of rootstock 4 the flower produced was the first one ever seen from this rootstock, which was originally collected on Point Reyes peninsula, and it is interesting to note that this flower, produced after six years of growth under different conditions of soil and climate, corresponds exactly in color and other characters (cf. Goodspeed and Brandt, 1916) to

those found during the same season in their native habitat. The evidence furnished by rootstock 11 and a number of others seemed for a time to indicate that there was each year an increase in the size and differentiation of the undeveloped flowers, and it was thought that this increase in size and differentiation would finally result in the production of a normally flowering shoot. As indicated, however, rootstock 11 produced a highly rudimentary undeveloped flower in 1915 after producing undeveloped flowers of larger size for a number of years. In general it seems plain that there is no gradual transition from undeveloped to normal flowers, but that a rootstock may produce a diminutive undeveloped flower in one season and a perfectly normal flower in the following season, just as the same rootstock might conceivably in a third season produce again a diminutive, undeveloped flower.

A further point must be noted in this connection. An offset produced from a parent rootstock never forms anything but an undeveloped flower in the first season in which it bears a shoot, and it is doubtful whether it produces a normally flowering shoot for a considerable number of years thereafter. A seedling rootstock has apparently the same history in this regard as the young offset. We are thus concerned with two rather different situations in connection with the occurrence of undeveloped flowers in *Trillium* species: first, the number of years of growth necessary in the case of offsets and seedlings for the production of a normal flower, and second, the number of years that must intervene, after a normally flowering rootstock has reverted to the condition of producing undeveloped flowers before a normal flower can again be matured. With reference to the first point, we have seen small offset rootstocks which when collected gave evidence of at least five years previous growth, produce only undeveloped flowers for six years in the garden cultures. As might perhaps be expected, it has been determined that seedling rootstocks in the field remain even longer in the undeveloped flower condition than do offsets from old, vigorous rootstocks. Concerning the second point above, we have, as can be seen in table 2, only one instance in the garden cultures—i.e., rootstock 39—in which a rootstock produced normal flowers, reverted to production of undeveloped flowers, and again after three years produced a normally flowering shoot. In the great majority of cases normally flowering rootstocks introduced into the garden cultures five or six years ago have thereafter borne only shoots with undeveloped flowers.

The problem of the occurrence of undeveloped flowers and its cause is further complicated by the fact that in *Trillium sessile* var. *giganteum* a vigorous rootstock may produce four or five shoots in a single season from its growing apex and all of these may bear normal flowers, all may bear undeveloped flowers, or one or two shoots may bear normal flowers and the remainder bear undeveloped flowers, this latter condition being by far the most common. The morphology of the growing apex of the rootstock, which is covered by heavy, protective, sheathing scales, will be dealt with in the following paper of this series and only certain points need to be mentioned here. There appears to be a critical stage during the active period below ground in the development of the buds at the bases of the sheaths of the rootstock "crown" such that if a given bud has not attained a fair degree of development by the first of July the growth of that bud is arrested and it may shortly thereafter die and shrivel up. It further appears that from a bud which has reached a somewhat more advanced but not the maximum development at the critical period a shoot with an undeveloped flower will appear the following spring. In other words there are three possibilities with reference to development of the buds following the critical period. First, the development of a given bud may be insufficient at the critical period and thus its growth ceases and it dies shortly thereafter. Second, a given bud may have reached the maximum degree of development possible at the critical period and thus successfully passes through this period and produces a normally flowering shoot the following spring. Third, a given bud may have reached such a stage of development at the critical period that further vegetative development is possible but the development of the floral primordia is not sufficiently advanced and growth of these structures is arrested or goes on very slowly to produce an undeveloped flower the following season. We may think of an intermediate stage between the last two, in which development is sufficient to allow of the formation of almost normal reproductive structures, the actual reproductive tissue failing of normal development.

The occurrence of a critical period is readily demonstrable. It appears to be connected with the shifting of a portion of the metabolic activity of the growing region, previously devoted to the formation of vegetative structures and floral primordia, to the development of reproductive tissue which takes place vigorously from July on to the period above ground. The occurrence of undeveloped

flowers is thus tentatively assigned to a lack of sufficient development of flower parts at the period when the products of metabolic activity stored in the rootstock are for a time shifted almost wholly to the reproductive tissues for their rapid development. A seedling rootstock or young offset is thus to be thought of as capable of maintaining nothing more than a vegetative existence above ground, a balance of available food properly to mature floral organs being accumulated in small amounts each year until after a variable but usually considerable number of years a normal in place of an undeveloped flower is produced. This explanation apparently covers such a case as that of rootstock 39 in table 2, since a rootstock which has successfully produced shoots should, other things being equal, be successful in passing from the condition of undeveloped to normal flower more rapidly than a seedling rootstock or offset which has never succeeded in producing a normal flower. The abrupt transition from normal to undeveloped flower production may be taken to be due similarly to a disturbance of metabolic relations, the most obvious of which is the taking up of a normally flowering rootstock during the height of its active period above ground. Such treatment almost invariably results in the production by it of an undeveloped flower in the following season.

In general, of course, the production of undeveloped flowers may be taken as an extreme instance of the sterility commonly seen in normally flowering plants of *T. sessile* var. *giganteum*, which produce very little viable seed and in which the pollen may be highly defective or the development of the pistil entirely suppressed. That the sterility found in normally flowering plants and expressed in its extreme form in the production of undeveloped flowers may be assigned to conditions of nutrition and available food-supply is at least suggested by a comparison of the reproductive methods of two distinct Californian species—*T. sessile* var. *giganteum* and *T. ovatum*. In the former, as we have seen, undeveloped flower production and sterility in normal flowers is common and here vegetative reproduction is important and very vigorously carried on (cf. Goodspeed and Brandt, 1916). In *T. ovatum*, on the other hand, viable seed is formed in a majority of the normal flowers; and undeveloped flowers, while common, are not produced in such amount, and finally we have hardly succeeded in finding a single instance of vegetative reproduction by offsets.

A variety of experiments are contemplated in an attempt to gain

positive evidence as to the cause of undeveloped flower production and the conditions both upon which it is dependent for continued appearance in the successive shoots from a rootstock and those which are responsible for the change back to the condition of normal flower.

Transmitted April 6, 1916.

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PLATE 5

Figures 1 to 6

Longitudinal sections through the apices of shoots of *Trillium sessile* var. *giganteum*, showing the nature of undeveloped flowers of different degrees of complexity.

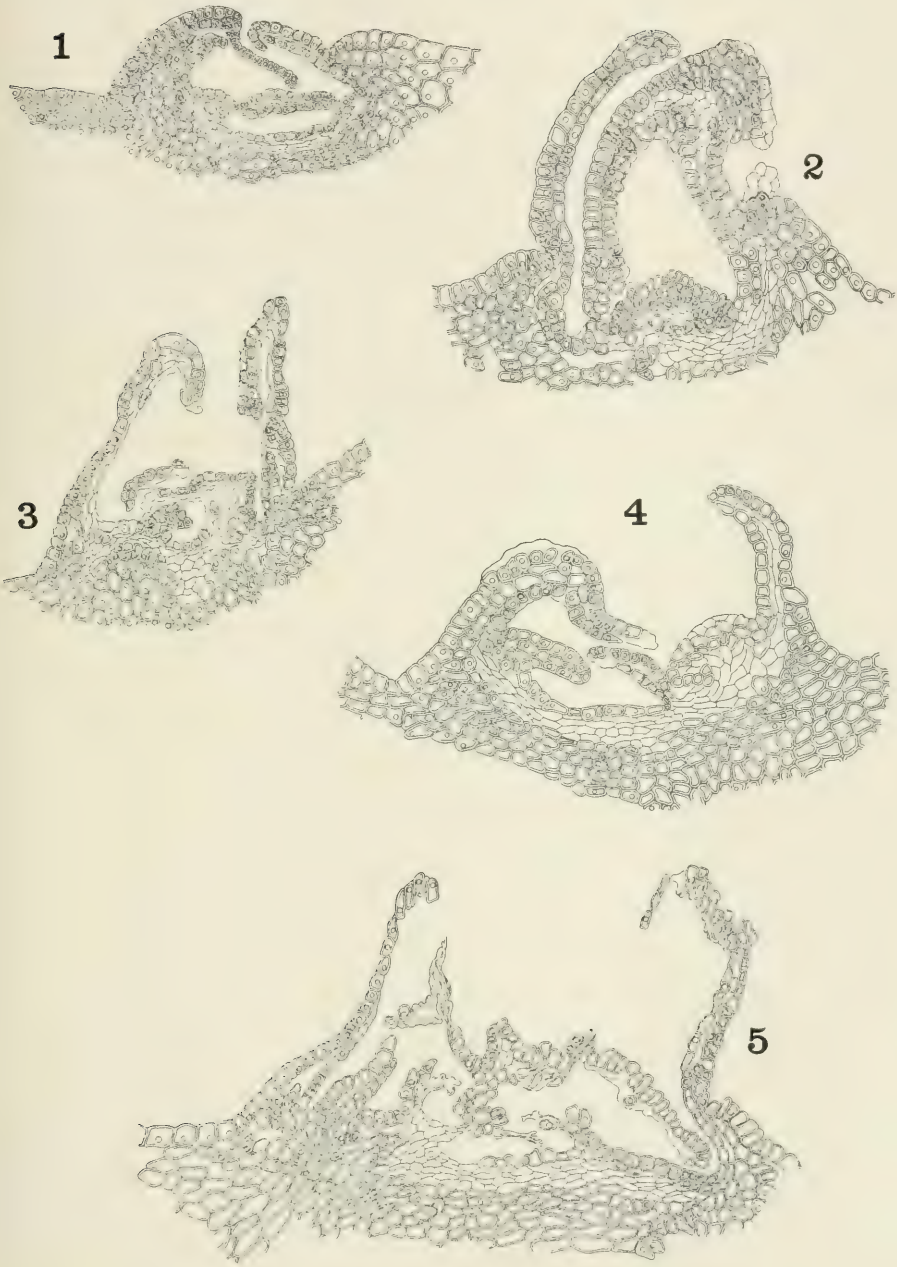
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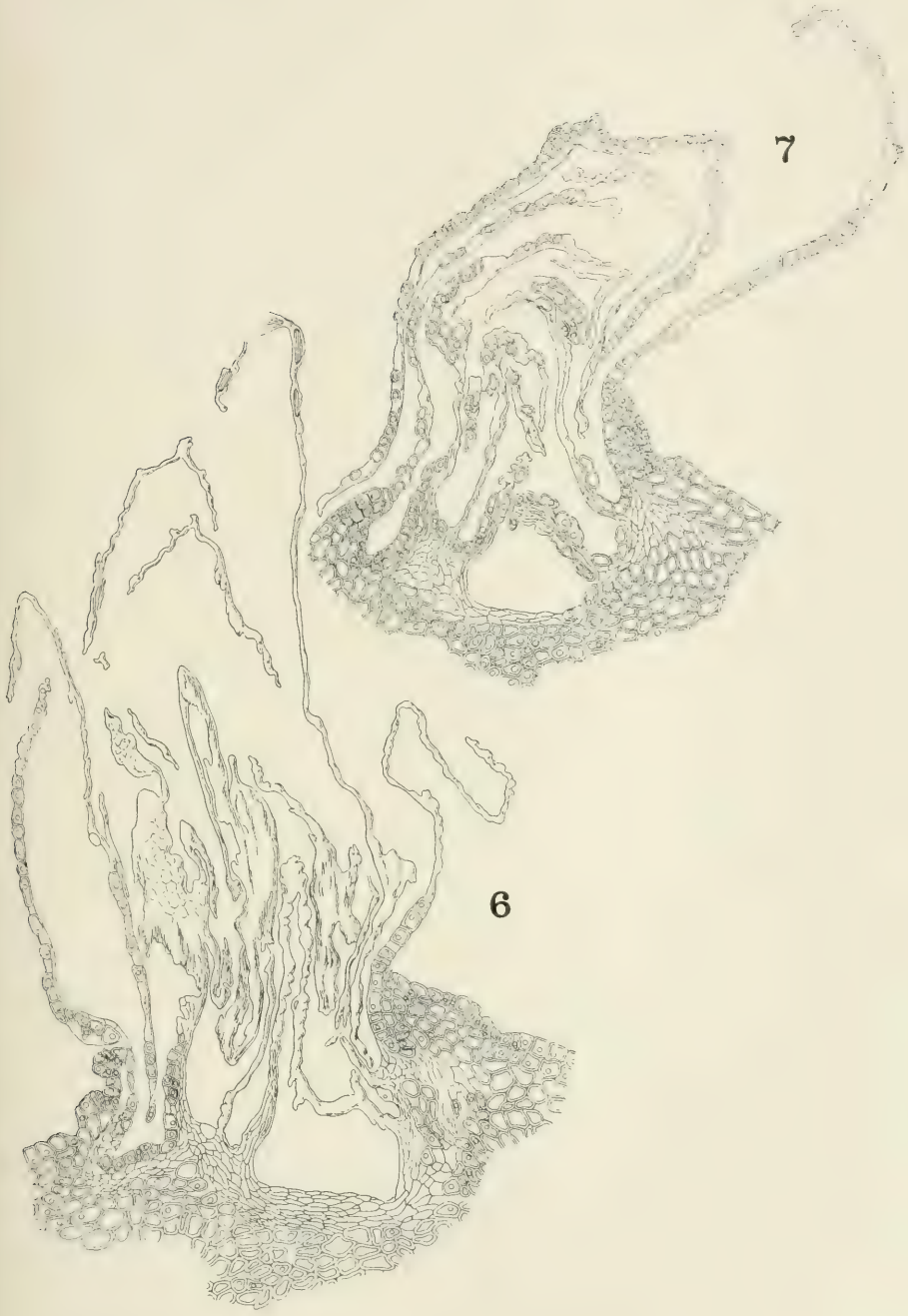
PLATE 6

Figures 7 and 8

Longitudinal sections through the apices of shoots of *Trillium sessile* var. *giganteum*, showing rather highly differentiated types of undeveloped flowers.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NOTES ON THE CALIFORNIAN SPECIES OF *TRILLIUM* L.

III. SEASONAL CHANGES IN TRILLIUM SPECIES WITH SPECIAL REFERENCE TO THE REPRODUCTIVE TISSUES

BY
ROBERT PERCY BRANDT

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I. Introduction

The variety of problems presented has made a study of the species of *Trillium* native in the region immediately surrounding San Francisco Bay of unusual interest and importance. The first two of the

studies in this series (Goodspeed and Brandt, 1916, *a* and *b*) were concerned with a general description of the Californian species of *Trillium*, with a brief mention of certain points in their life-history and a discussion of the origin, nature and significance of the widely occurring undeveloped type of flower. The present paper, the third in the series, is particularly concerned with the condition in which these western species pass their resting period, a period apparently determined by available moisture. The matter seemed of special value since information is furnished by the literature concerning the condition of eastern species during a corresponding dormant period in which both moisture and temperature relations are seemingly concerned.

Chamberlain (1898) reports that spring-flowering perennial plants either pass the winter in the spore mother-cell stage or mature their spores before the winter season, but with the data at hand was unable to decide which was the more general condition (cf. Pfeiffer, 1912). Among those plants which pass the winter in the spore mother-cell stage he includes *Trillium* species, on the basis of the report of Miss A. M. Smith (1896), who found that the pollen mother-cells were "in the early stages of division" in a specimen dug from beneath the frozen soil on April 5. She found the "later stages of division" and pollen fully matured on April 15, when numerous plants were appearing above ground (cf. Gates, 1908, p. 46). Atkinson (1899), working on *T. grandiflorum* (Michx.) Salisb. in the vicinity of Ithaca, New York, where Smith had previously worked, reports that in all plants he examined the pollen mother-cells were formed by the beginning of winter, and that in open woods on rather high ground, protected from north and west winds, pollen was often mature in September. In cold ravines, on the other hand, plants entered into the resting period in the pollen mother-cell stage. Late in February and early in March, when the weather is relatively warm, formation of pollen begins. The report of Ernst (1902) dealing with the condition of *Paris quadrifolia* L. and *Trillium grandiflorum* tends to confirm that of Smith, noted above. He states that micro- and megaspore mother-cells become plainly distinguishable toward the beginning of the growing season, late in February or early in March. Chamberlain (1898) also reports four potential magaspores fully formed in April on a plant of *T. recurvatum* Beck. not more than 5 cm. high. The above reports show that *Trillium* species native in the Eastern United States and cultivated in gardens in Northern Germany usually mature

their spores in the early part of their growing season before or shortly after the young shoots appear above ground. Miss Alden (1912) gives a review of the rather meager literature on this general subject in connection with her pertinent study of stages in the seasonal development of *Uvularia sessilifolia*. Howard (1915) has made a series of interesting experiments in an effort to break the summer rest period of bulbous plants.

With the object, then, of finding out how nearly the behavior of our forms of *Trillium* in the resting season agreed with that of the eastern forms, collections and observations were begun in the autumn of 1913. Collecting was begun while the plants were in the pollen mother-cell stage, late in September, and was discontinued in April, when most of the plants were going out of flower. Collecting was resumed in August, 1914, and continued until November 10, 1915.

Most of the material was collected in the hills near Berkeley, on the eastern side of San Francisco Bay, but from the latter part of May to the early part of August, 1915, *T. sessile* var. *giganteum* H. & A. was collected at Point Arena, Mendocino County. From time to time *T. ovatum* Pursh was collected for purposes of comparison, at Mill Valley, Marin County, and at Gualala, Mendocino County.

Up to the autumn of 1915 all specimens were trimmed and killed in the field to avoid wilting. In these last collections, made for the express purpose of securing a large supply of material showing chromosome reduction in the pollen mother-cells, the material was brought into the laboratory and examined before killing, suitable precautions having been taken to keep it fresh. The following killing solutions were used: Bouin's solution, Zenker's mixture, Flemming's fluid (strong), and Farmer's absolute alcohol-acetic acid solution. The last two gave the best results.

All material was imbedded in paraffin. Anthers were sectioned 7 to 10μ thick, ovaries 7 to 25μ, according to the stage of development of the ovule, and young stems just forming lateral organs were sectioned 10 or 12μ thick. The stains used were aqueous safranin and Delafield's haematoxylon in combination or alone; safranin and "light green"; the safranin, gentian-violet, orange G. combination; and Haidenhain's iron alum haematoxylon. The last stain was particularly useful in studies of chromosomes, while the most generally successful was the safranin "light green" combination.

II. The Subterranean Organs of Trillium Species

The storage structure of *Trillium* consists of a stout subterranean stem provided with a relatively large terminal bud, or "crown," and perennial roots. In shape the rootstock of *T. sessile* var. *giganteum* is usually nearly cylindrical, but tapers slightly to one or both ends. It varies in length from 3 to 8 cm. and in diameter from 2 to 5 cm. or more. The rootstock of *T. ovatum* is more slender, varying in length from 2 to 4 cm. and in diameter from 5 to 15 mm. (cf. Rimbach, 1902). In both species the rootstock is either erect or horizontal. When the rootstock is buried deeply it usually stands erect, as Rimbach (*loc. cit.*) states for *T. ovatum*. Often, as noted by Rimbach, the rootstock of *T. ovatum* may grow sharply downward at the crown end, and thus the erect terminal bud makes an acute angle with it.

Since the rootstock in general grows only enough to make room on its surface for the bases of bud sheaths and axillary structures, the annual growth is slow, probably never more than two centimeters. Rimbach states that the rootstock of *T. ovatum* does not grow more than 1 mm. per year, but I have seen specimens that showed indication of an annual growth of 2 mm. or more. The scars on the surface left by the decay of the bases of aerial shoots furnish a good indication of the amount of annual growth, but when a plant sends up several shoots per year one must depend more upon the slight annual constrictions of the rootstock, which are often readily discernible. As growth goes on at the "crown" end of the rootstock the base rots away, generally leaving a smooth scar; the age of the living portion of the rootstock does not thus necessarily indicate the actual age of the plant. Rimbach further states that the rootstock of *T. ovatum* sometimes contains the living product of twenty to forty years' growth, but that is far too great an estimate. Carl Purdy, the well-known horticultural authority on California *Liliaceae*, informs me that in his experience Trillium rootstocks seldom persist entire for more than fifteen years even in well drained gravelly soil, and in ordinary garden soil the rootstock of *T. sessile* var. *giganteum* contains the living product of less than five years' growth. It would seem that Rimbach, who collected his material on the slopes of Mount Tamalpais, Marin County, must have based his conclusions as to the persistence of rootstocks upon the rate at which young rootstocks grow during their first four or five years. The evidence furnished by my own collections made in the same locality and elsewhere confirms the statements of

Purdy mentioned above. My determination of the age of a given rootstock is made by counting the scars left by the decayed bases of aerial shoots and noting the slight annual constructions which usually can be seen on the surface of the rootstock.

Roots grow out from the lower side of a horizontal rootstock, but when the rootstock stands erect the roots grow out equally from all sides (cf. Rimbach, *loc. cit.*). Rimbach states that *T. ovatum* produces two or three roots per year, and that they live eight or ten years, so that the plant may have as many as twenty roots, but he probably overestimates the age of the roots just as he does that of the rootstock. *T. sessile* var. *giganteum* sends out three to five or more roots from near the base of the terminal bud or "crown" at about the time the young shoots appear above ground. These attain a length of 15 to 20 cm. or more the first year. During the second year they increase their length still more and send out fairly numerous branches of the first order. They apparently live three or four years, or even longer, but probably not so long as the portion of the rootstock which bears them. When the roots have attained a considerable length, they begin to contract, the surface of the roots becoming noticeably wrinkled as they do so. This contraction draws the rootstock down into the ground. Since only the young roots contract, the pull is exerted only at the growing end of the rootstock. If the ground is hard this will cause the young rootstock, upright in the young seedling stage, to become inclined from the perpendicular. As the rootstock becomes inclined it develops a tendency to send out roots only from the lower side, thereby eventually becoming horizontal or inverted. Evidence of this gradual change of position of the rootstock is furnished by the slight arching so common in that of *T. ovatum*. On the other hand, the rootstock tends of itself to assume an upright position, so that in loose soil upright rootstocks may be found. When the rootstock is erect, roots, as noted above, grow out equally from all sides, and thus enable it to maintain an upright position.

As a result of this tendency of the rootstock to grow erect and to send out roots more nearly in all directions the more nearly erect it becomes, we find most of the rootstocks of *T. sessile* var. *giganteum* and the stronger ones of *T. ovatum* growing erect or curving upwards. Rimbach states that the roots of *T. ovatum*, which attain a total length of 20 to 30 cm., reduce their length about 1 cm., becoming wrinkled for a distance of 3 or 4 cm. in doing so. The roots of *T. sessile* var. *giganteum* show this same surface wrinkling. Photographs of root-

stocks are included in a previous report (cf. Goodspeed and Brandt, 1916, *a*, pls. 1 and 5).

The terminal bud, or "crown," suggests a large aerial winter bud as much as it suggests the bulb of a lily. It is more or less elongated and conical, with a diameter somewhat less than that of the rootstock. The sheathing scales, each of which completely enwraps all the parts inserted above it, are thin and tough, adapted to protective purposes

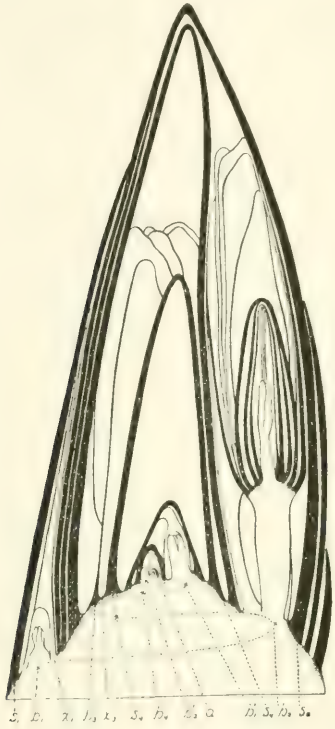

Fig. 1

rather than serving as starch-storing tissue. Figure 1 above illustrates the structure of a strong "crown" early in September. s_1 is the outermost sheathing scale, not quite reaching to the top of the crown, brown and dry; bearing in its axil a spongy, scale-like body, x_1, which in turn has an aborted stem-bud, b_1, in a socket in its base. s_2 is a large living sheath which envelops the crown, folding completely over it but not fusing along its margins. The bud b_2 is the largest in this crown. It has grown up out of the "axillary sheath or scale-like body" and is pressing it back against the next protective sheath. It

will be noticed that the leaves greatly surpass the sepals and are folded several layers thick around the flower-bud and the anthers at this time practically fill the space in the center of it. Vascular bundles are plainly distinguishable in the young stem. b_3 is the second normal bud, which is shown entire. As in b_2, the young foliage leaves completely enwrap the flower bud. The size and shape of the "axillary sheath" is illustrated by x_3. Sheath s_4, as will be noted, is considerably shorter than bud b_3, so bud b_4 would naturally be much smaller than b_3. Only the position that bud b_4 would occupy can be indicated. Bud b'_1 will be noted under a very short, young sheath. This bud if shriveled up would be a trifle smaller than b_1, and perhaps a little less advanced. It is not a bud for next season, but for the season following, when it will fail of development in the same way as b_1. b'_2 is barely distinguishable, and at a the apex of the rootstock is covered by a few young sheaths which are merely arched and have no buds, only "axillary sheaths," in their axils.

It is important to note the abortion of b_1 and the possible abortion of b'_1. Apparently all the buds from b_3 and inward were laid down in the preceding active season, but b'_1 and b'_2 were arrested in development so that they could not become shoots during the next season. There is apparently a critical period during which further development in the younger buds is temporarily suspended. Examination of a crown late in May seemed to show that there is a selective elimination relative to the amount of differentiation the various buds exhibit. Thus, as a general rule, the bud which fails during this critical period to meet the requirements of sufficient growth dies and shrivels up later on. In very strong plants of *T. sessile* var. *giganteum*, those which send up four or more shoots in a season, the largest arrested bud develops into a shoot, usually smaller than the one next within. In very large plants this outer shoot may show increase in number of parts or may even become fasciated. A report upon numerous teratological forms peculiar to *T. sessile* var. *giganteum* is in progress of preparation.

The "crown" of *T. ovatum* is very similar in structure to that of *T. sessile* var. *giganteum*. Usually not over two buds are formed each year instead of two or more, as in the latter species. The first of these fails to develop. When the plant is given an unusual amount of light both buds develop into strong, normal shoots. Because of its habit of forming two buds a year, one may often find *T. ovatum* in partially cleared forest areas regularly sending up two shoots from one root-

stock. Plants with three or four shoots are always in the minority, whereas there seems to be no limit to the number of shoots that a single rootstock of *T. sessile* var. *giganteum* may send up, eight having been seen in one specimen.

In addition to the parts enumerated above, the rootstock of *T. sessile* var. *giganteum* very frequently has one or more young rootstocks growing out from it as lateral branches or "offsets." These increase their diameter from year to year, build up their own root systems, and by decay of the older portions of the rootstock soon become independent plants. In this way a single plant often in time produces a clump of a dozen or more. On the other hand, *T. ovatum* very rarely produces an offset (cf. Kerner and Oliver, 1895, pp. 452-454). The general significance of vegetative reproduction in *Trillium* species has been fully discussed in a previous report (Goodspeed and Brandt, 1916, *a*).

Foerste (1891) states that the Eastern or type form of *T. sessile* L. is characterized by a horizontal rootstock, and refers to the orientation of the rootstock by the contraction of the roots. He also states that in early winter there are buds present in the rootstock crown for two active seasons in advance.

III. The Active Period, February to July

1. ABOVE GROUND

a. Trillium sessile var. *giganteum*

In a previous report (1916, *a*) we have fully outlined the climatic conditions under which plants in western middle California pass their annual life-cycles. A number of the points there emphasized are of importance in the following discussion and will be briefly referred to.

Trillium sessile var. *giganteum* appears above ground in the latter part of January and in February. This species has withered and in almost all cases disappeared by the end of July. For convenience I have chosen to regard this period—February to July—which includes the life of the plant above ground as equivalent to the "active" period. It is of course obvious that the active period of growth and flowering occupies a considerably shorter interval. However, the period chosen covers the interval from the appearance of the green shoot to the shedding of seed, and therefore marks the life-cycle above ground.

When the young shoot first appears above ground the leaves are tightly rolled into a cone about the flower-bud. In some plants the

leaves are imbricated in the bud, in others convolute, the species apparently not adhering to one arrangement. The characteristic colors of the various aerial parts are variable in the time of their appearance. As the shoot emerges, the leaves and sepals rapidly change from deep yellow to green, while the petals attain their full coloration only when entirely exposed to the light and free from the enveloping sepals and leaves. The stamens are heavily pigmented, showing almost their full coloration a short time before the flower unfolds.

From the first appearance of the tip of the shoot above ground to the complete emerging of the tightly rolled cone of leaxes approximately a week intervenes. Thereafter growth is rapid until the maximum length of stem is reached. Measurements made on developing plants in the University of California Botanical Garden, and field notes, provide the basis for this statement. Almost with the start of this rapid growth to increase the length of the stem a loosening of the cone of leaves is evident, and as growth proceeds the unfolding of the leaves is sufficiently rapid so that they are completely flattened shortly after the maximum height is attained. This gradual unfolding and flattening of the leaves is accompanied by a sufficient increase in size so that they are nearly mature, so far as growth and expansion are concerned, when the stem has attained its full height. In general it might be said that this period of rapid growth occupies, in average cases, a little more than two weeks.

The significant stages in the development of the flower take place subsequent to the complete unfolding of the leaves. The sepals are practically full size at this time and are pushed apart by the rapid growth of the petals, which are hardly in sight within the sepals when the leaves first unfold. The petals are fully mature and the flower unfolds approximately three weeks after the shoot first appears. Owing to the method of dehiscence of the pollen sacs, anthesis may follow immediately or after an interval of more than a week, according to atmospheric conditions. Dehiscence is accomplished by the mere straightening of the walls of the locules, caused by the epidermis contracting more than the endothecium. The locules may remain distinct until anthesis, in which case a zone of small-celled tissue is developed between the locules (see pl. 10, fig. 2), or they may become fused into one by the disintegration of the parenchyma between and back of them, but this is not essential to dehiscence. It can be shown that anthers from unopened flower-buds may dehisce within an hour in the dry air of the laboratory.

When the flower first opens the stout styles are erect and closely pressed together. Gradually they roll back at the tips and also spread apart at other points below, but never spread apart very widely. The markedly papillose surface of the stigma is very undulate. This probably aids in pollination in two ways, by increasing the surface area and by providing hollows and pockets in which pollen may lodge.

The anthers show more or less tendency to curve over the stigma, sometimes forming a close cone over it, although in other cases they are somewhat divergent. As they open introrsely self-pollination is in most cases inevitable. The flower is rarely visited by insects (cf. Carter, 1892).

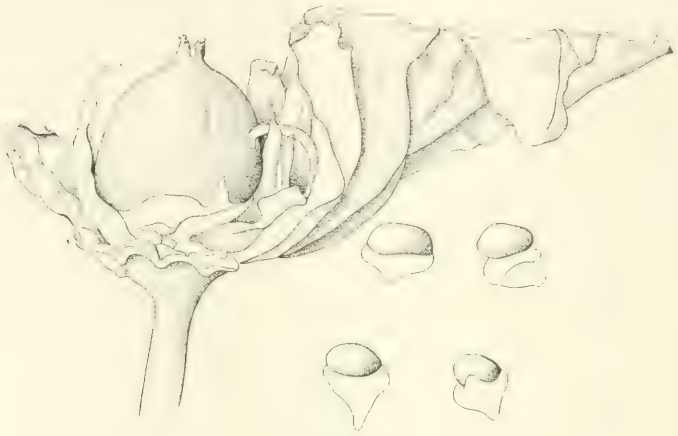

Fig. 2

In from three to six weeks the petals and stamens wither, but do not fall. Sepals and foliage leaves persist until the fruit ripens, or the leaves may perish earlier. As has already been stated, the fruit ripens late in July. It varies in shape from elongate-oval to slightly spheroid, 15 to 35 mm. long by 12 to 34 mm. thick; is terete at the base, slightly six-angled above, with the persistent bases of the styles forming three short beaks. The color varies from pale green without a purplish tinge to red or purple. The fruit dehisces by breaking away at the base and tearing up one side (fig. 2). The seeds are usually numerous, sometimes numbering nearly 200, are 4 mm. long by 2 mm. thick, oval, light brown; with fleshy white aril larger than the seed, developed from the funiculus (fig. 2). This aril is greedily eaten by ants (Robertson, 1897, p. 288). So far as I am aware, this is the first complete description of the fruit of the western ally of *T. sessile* L.

b. Trillium ovatum

Practically all the points noted above in the description of the active period above ground peculiar to *Trillium sessile* var. *giganteum* hold in modified form for *T. ovatum*. It might be recalled that *T. ovatum* is a pedunculate species in contrast to *T. sessile* var. *giganteum*, which is sessile, and that previous to anthesis the flower is white. Growth is much more rapid, the shoot attaining full height in a week. The flower opens before the leaves are fully spread and the petals have faded and fallen by the time the plant has been out of the ground a month. The species is distinctly protandrous and is doubtless entomophilous, as Robertson (1896) states is the case in *T. grandiflorum* and *T. erectum*. Little need be said about the fruit, which usually ripens in May, except that dehiscence is septicidal, beginning at the apex and extending to the base. The seeds, which are smaller and darker brown than those of *T. sessile* var. *giganteum*, sometimes number more than 300. They also are myrmecophilous, as Robertson (1897) reports for *T. recurvatum*.

2. BELOW GROUND

a. Trillium sessile var. *giganteum*

With the beginning of growth in February the bud-sheaths lengthen sufficiently to appear a few centimeters above ground and protect the young leaves as they push up through the soil. They are separated by the rapid growth of the young shoots and gradually disappear. The axillary "sheaths," or spongy bodies at the bases of the main sheaths, lengthen but little, but appear to remain alive quite late in the flowering season. At this same time the apex of the rootstock begins to grow and to lay down new stem-buds while the young buds whose growth was suspended resume development, with the exception of the first bud, which now shrivels up, as previously stated.

The young stem is at first a short cylinder of undifferentiated parenchyma. Soon the lateral structures make their appearance in acropetal succession. The young axis is produced beyond the point of insertion of foliage primordia so that the young sepals slightly overtop them at first (pl. 7, figs. 2 and 5). During early development the floral organs apparently grow more rapidly than the foliage leaves, so that a bud examined in May would give one the impression that the sepals begin their growth before the foliage leaves.

By May 1, in at least the most advanced bud, sepals and petals have completely closed over the parts within (pl. 7, figs. 3 and 6).

At this time the young flower-bud averages 2 to 3 mm. in length, the size of the bud and the degree of development apparently varying considerably, according to the strength of the plant. The anthers by this date practically fill the interior of the flower-bud. In general the second bud in the "crown"—the first, as noted above, being functionless—is the largest and most highly differentiated, each successive bud thereafter being two weeks or more behind its immediate predecessor.

What appears to be the critical period in development at which the apex of the rootstock ceases to grow and the buds nearest it are arrested in their development occurs late in May. Buds seem to gather momentum in their development, so that those which have their primordia well advanced before this critical period go on developing, while in the case of those which are not sufficiently advanced further development is suspended until the following year. As has been stated above, when the development of a bud which has formed its primordia is sharply arrested the result is usually fatal, still younger buds (fig. 1, b'_2) not so well differentiated are usually able to resume growth upon the arrival of the next active season. Small plants that form only two buds and send up one shoot a year thus lay down their buds nearly two years in advance. On the other hand, those plants which send up four or more shoots a year begin to form some of their buds one season and the others two seasons before they are to appear above ground.

In June and July, following the period of suspended activity, the entire terminal bud of the rootstock, or crown, is growing with maximum rapidity. All parts are increasing rapidly in size at this time, but most noticeable is the renewed activity of the young foliage leaves. They increase in size more rapidly than the young flower-buds and overtop them by the latter part of July (pl. 7, figs. 4 and 7). There is still a striking inequality in size and in degree of development among the various buds, but by the middle of July, or earlier, the youngest or innermost bud for next season is larger and better differentiated than the oldest or outermost was in May. Sometimes when only two buds are developing for next season they are nearly equal in size and in degree of differentiation, and when the outermost—usually functionless—bud (cf. fig. 1, b_1) develops in addition to the others it is very likely to be smaller than its immediate successor. It seems that the checking of development of a bud as far advanced as this outermost bud always is at the critical period has a much more per-

manent effect than the checking of a bud less advanced. This outermost bud, in the relatively few cases when it thus actually develops, tends to produce a smaller flower and seems less likely to produce a fruit than the next. This statement is based upon field observations. Because of the great increase in size of the buds for the next season it becomes very easy from this time on to distinguish those whose development has been arrested.

Somatic divisions are taking place in all parts of the young buds, but more especially in the anthers. From the middle of May to the middle of June the archesporial cells of the anthers are cut off (pl. 7, fig. 8). In an anther of *T. sessile* var. *giganteum* there are usually four rows of archesporial cells. These closely resemble the adjacent cells, but may be recognized by their larger size, radial elongation, and position immediately under the epidermis. They soon begin to divide to form sporogenous and parietal tissue. As development progresses the differences between sporogenous and parietal cells become more and more noticeable. All the parietal cells which are arranged in layers are greatly flattened as a result of periclinal division, their cytoplasmic content is not very abundant and their nuclei are relatively small but rich in chromatin. The sporogenous cells, on the other hand, are not arranged in layers and have no definite form. They are non-vacuolated and their cytoplasm shows a reaction to stains different from that of the cytoplasm in other cells of the anther. Their nuclei are large, but rather less densely filled with chromatin than those of the parietal cells. There is therefore a great difference in appearance between sporogenous and parietal cells, but the tapetum is not yet cut off. Late in July the ovules begin to make their appearance as slight protuberances of the placentae, but their archesporial cells do not appear until later in the year.

b. Trillium ovatum

Practically the same series of phenomena reported above for *T. sessile* var. *giganteum* occurs during this active period below ground in *T. ovatum*, but a few exceptions should be noted. Mention has been made of the fact that fewer buds are formed in *T. ovatum*, the number being limited to two in average cases. It might here be noted that the peduncle becomes noticeable before the flower-bud has attained one-fifth of its mature length. The most noticeable difference is in the rate of development of the floral organs. In some specimens young pollen grains are present before the last of July. This very

early appearance of pollen in *T. ovatum* has a parallel in those plants of *T. grandiflorum*, reported by Atkinson (1899), whose pollen was fully matured in September. It is also interesting to note here two statements which have been made with regard to the size of the flower-bud in Eastern species of *Trillium* the season before flowering. Foerste (1892) states that the largest bud of *T. erythrocarpum* Michx. which he collected in Connecticut in August was 5.5 mm. long, quite comparable in relative size to buds of *T. sessile* var. *giganteum* in June. Smith (1896) states that a flower-bud of *T. grandiflorum* found in central New York on July 11 was 2 mm. long with anthers 1.7 mm., such a bud as one can find in *T. sessile* var. *giganteum* early in May.

IV. The Dormant Period, August to January

a. Trillium sessile var. *giganteum*

The season from August to January inclusive is to be called the dormant season, in the present paper. The term "dormant season" is again used here simply for convenience, just as the term "active season" is used to designate the season from January to July inclusive. Many plants, as previously noted, cease their activity above ground in May or earlier, while, on the other hand, others are appearing above ground in November or earlier. Generally speaking, however, the season from August to January inclusive is the season in which *T. sessile* var. *giganteum*, growing in the vicinity of San Francisco Bay, has no green leaves above ground.

This season may be divided into two parts, a season of decreased activity and a season of increased activity. The first division continues until the beginning of the rainy season, late in September or early in October. As noted above, the period May to July is one of active and continued growth, resulting in the differentiating out of the floral organs. During the period August to late September, the dryest season of the year, development is practically at a standstill, while with the opening of the rainy season growth becomes even more rapid than during the period May to July. The period of decreased activity is, however, characterized by the cutting off of the pollen mother-cells and a resting stage preliminary to their rounding up and entering upon the prophases of the meiotic divisions. The last somatic divisions in the sporogenous tissues, giving rise to the full number of pollen mother-cells, are completed in the latter part of August and

early part of September. The anthers are at this time almost fully grown and nearly fill the interior of the flower-bud. The pollen-sacs, which are still nearly colorless, are also very slender, owing to the fact that the pollen mother-cells are not rounded off. They are very angular in outline and, when crushed out of a living anther, cohere firmly in a mass. The cytoplasm is dense and the nuclei are very large. From one to three nucleoli are present and the open reticulum is composed of thinly scattered chromatin granules (pl. 8, fig. 1). The tapetum is definitely cut off, but its cells have not as yet become so greatly enlarged as they appear in a mature anther, nor have their nuclei divided.

The pollen mother-cells continue in the resting stage for four weeks or longer before rounding off and preparing to divide. At about the middle of September or early in October, when the rainy season begins and the weather becomes cooler and the soil contains some moisture, the underground organs of *Trillium sessile* var. *giganteum* begin to show increased activity. This increase is manifest first in a lengthening of the protective sheaths of the crown, and then in an increase in size in all the parts of the stem buds for the next active season. There is a very noticeable change in the appearance of the anthers. Their length does not increase very appreciably, but the pollen-sacs begin to increase rapidly in diameter and their color begins to change from nearly white to pale yellow—the color of pollen-sacs in which the reduction divisions are taking place—and finally, as the pollen attains maturity the color becomes deep yellow. When examined under the microscope the pollen mother-cells are found to be rapidly increasing in size and their nuclei show a more than proportionate increase (pl. 8, fig. 1). In some locules pollen mother-cells are in synapsis, while in others, even in the same anther, the chromatin is still distributed in the form of rather large granules throughout the nuclear cavity. These "resting" nuclei are fully as large in diameter as are those in synapsis (see pl. 8, figs. 1 and 2). I have not found such an increase in size of the nuclear cavity during synapsis in *Trillium* as Lawson (1911) reports in *Smilacina*.

The statement has already been made that in the same flower-bud, or even in the same anther, in *T. sessile* var. *giganteum* the pollen mother-cells in one locule may be in synapsis, while in another the chromatin still forms an open reticulum. It may be well here to state that the period during which the meiotic divisions occur extends over two months—October to November—a condition in striking contrast

to that which Atkinson (1899, p. 10) found in *T. grandiflorum*, where "the period during which the division of the pollen mother-cells takes place extends over seven or eight months." As in *T. grandiflorum*, the time of division of the pollen mother-cells varies with the season, the location, and the degree of development of the other parts in the individual. As noted above in the case of large plants which produce a number of buds during the active season below ground, any two buds may be strikingly different in the amount of development which they exhibit during the month of May. By October or November this discrepancy in development appears to have been made up and the reduction division takes place much more nearly simultaneously in the various flowers of a rootstock than might have been anticipated. It seems clear that approximately six weeks elapse in average cases between the synaptic condition and the cutting off of the generative nuclei. Of this period of six weeks, the first three include the stages intervening between synapsis and the homotypic division and the remainder are occupied by the stages between the homotypic divisions and the cutting off of the generative nuclei.

Mention has already been made of the rapid growth of the pollen mother-cells and their nuclei previous to synapsis. The locule also may often increase so rapidly in size that the pollen mother-cells come to lie in a mass in the middle of a large cavity. During synapsis the chromatin often becomes so completely contracted that all semblance of structure disappears. It is during this stage apparently that the nuclei of many pollen mother-cells degenerate, cytoplasm and cell-walls disappearing shortly thereafter. During the later prophases of the heterotypic division the nuclear membrane seems to disappear and the pollen mother-cells round up. Atkinson (1899, p. 12) states that the double nature of the broad chromatin band is indicated by the presence of a double row of dense bodies. In the material at hand it was not possible to distinguish many granules in the bivalent chromosomes because of thickness and density of the latter, but evidence of their double nature was furnished by the occasional appearance of a longitudinal split while they were in the equatorial plate stage. In the metaphase the chromosomes are arranged in a nearly flat equatorial plate as Vs whose free ends stand out around the spindle (pl. 9, fig. 1), as Ernst (1902) reports for the megaspore mother-cell in *Paris quadrifolia* and *Trillium grandiflorum*. The spindle fibers are attached to the chromosomes at the apices of the Vs, the chromatin becoming drawn out thin at the point of attachment, as Atkinson

reports for the heterotypic mitosis in *T. grandiflorum*, and as Gregoire (1912) reports for somatic mitoses in the same species and in *Galtonia*. As the chromosomes migrate to the poles they gradually divide and before the cross-wall is formed in the equatorial region twelve separate chromosomes may be found in each polar group. They are much more slender than the bivalent chromosomes, are irregular in outline, and a single row of granules is plainly discernible. The spindle fibers disappear and a cross-wall is formed before the homotypic spindle fibers appear, but a true resting stage was not found, such as Ernst (1902) reported to intervene between the heterotypic and homotypic divisions in the megaspore mother-cell of *Paris*. My results seem to confirm those of Atkinson in this matter. The homotypic division takes place so rapidly that I have been unable to obtain preparations showing stages earlier than the polar groups of six chromosomes each. Soon after the homotypic division has been completed cross-walls are laid down to form the tetrad.

The tetrads soon break up into very angular young pollen grains whose non-vacuolate cytoplasm appears to be very compact. Soon the pollen grains begin to round out, but at no time in their development does their cytoplasm become vacuolated, as Dorsey (1914) reports is the case in *Vitis* species. As stated above, in approximately three weeks after the homotypic division many of the pollen grains have attained maturity, the exine has its characteristic markings, and the nuclei are dividing. The microspore nuclei do not divide with the uniformity in regard to point of time characteristic of pollen mother-cells, and only a few division figures may be found at any one time in a given locule (pl. 10, fig. 1). Many pollen grains in this species never round up properly and many others are less than the normal size.

The cells of the tapetum attain their maximum size when the pollen mother-cells are in the tetrad stage. Their nuclei are very large and very rich in chromatin. When they divide, the chromosomes—having apparently the full somatic number—form a very compact division figure. Variations from the binucleate condition have not been found. As the young pollen grains mature the cells of the tapetum gradually lose their contents and become flattened against the outer layers. Pollen sterility is often anticipated in an abnormal condition of the tapetum, which may become separate from adjacent parietal layers or may begin to degenerate before the pollen mother-cells divide. Other tissues of the anthers also degenerate. Most frequent is the degeneration of the tissue between adjacent locules, which may include the

epidermis and eventually aid in dehiscence. As the tapetum degenerates anther sap appears and sometimes is very abundant when the pollen grains are about half grown, but disappears soon after the division of the microspore nucleus. From the early part of December to anthesis, late in February, no changes take place in the appearance of normal pollen. During this period, however, the cells of the endothecium are increasing their radial diameter and develop radial thickenings on their walls (pl. 9, fig. 2). The method of dehiscence of the anther has been described above.

At the time when the pollen mother-cells are dividing the ovules already have the nucellus and the integuments well differentiated (cf. Coulter and Chamberlain, 1903, p. 52). The megaspore mother-cell is discernible in the third layer of cells immediately under the apex of the nucellus. It may be recognized by its slightly increased size, nearly square shape, and large nucleus with rather open reticulum (pl. 7, fig. 9). Nucellus and integuments grow with gradually increasing rapidity until the arrival of the flowering season, but the megaspore mother-cell changes but little in size and appearance at the time the shoot appears above ground (cf. Alden, 1912, p. 443). As the stem and leaves begin their rapid growth above ground the megaspore mother-cell begins to grow rapidly and take on an elliptical form. When the leaves are becoming fairly well unfolded the heterotypic division occurs (pl. 7, fig. 10). Sufficient material was not obtained for a critical study of this stage and the succeeding stages in the formation of the embryo-sac, but from the fact that the heterotypic division takes place after the shoot has appeared above ground and that a large embryo-sac is present when the flower unfolds it seems safe to assume that the female gametophyte in *T. sessile* var. *giganteum* follows practically the same course of development as Ernst describes for the female gametophyte in *T. grandiflorum*.

Actual confirmation of Ernst's conclusions can be made only with regard to the earlier stages in the maturation of the female gametophyte. Thus I have seen the formation of the cross-wall following the first or reduction division of the megaspore mother-cell (cf. pl. 1, fig. 10). This wall is curved and arches upward as the inner cell develops at the expense of the outer (cf. Ernst, 1902, p. 14, pl. 5, figs. 143 and 144). The inner, persistent cell enlarges, takes on an oval form and becomes the young embryo-sac (cf. Heatley, 1916). During its increase in size free nuclear division takes place to produce first a binucleate embryo-sac. Ernst reports that the young embryo-sac con-

tinues in this binucleate condition for two weeks or more (*loc. cit.*, p. 20).

b. Trillium ovatum

As noted above, *T. ovatum* matures its pollen earlier in the season than *T. sessile* var. *giganteum*. In general the pollen mother-cells divide during August and September, and pollen is apparently mature in all plants by the first of November. By the latter part of December nucellus and integuments apparently have attained nearly their mature size, and it seems probable that growth of the female gametophyte begins before the shoot appears above ground. As in *T. grandiflorum*, the megaspore mother-cell in *T. ovatum* becomes centrally located in the nucellus.

V. Summary

1. The underground structures of a *Trillium* plant consist of a stout subterranean stem, or rootstock, bearing perennial roots and a large terminal bud. As the rootstock adds live tissue at its growing end from year to year the basal end decays. Thus at any one time the rootstock, instead of representing the actual age of the plant, represents only a portion of its age, three to fifteen years, according to the rate of decay.

From two to five or more roots are sent out each season, according to the size and vigor of the plant, and live from two to ten years. By contraction they draw the rootstock down into the ground, and, usually in the case of *T. ovatum* Pursh, sometimes in *T. sessile* var. *giganteum* H. & A., orient it in a horizontal direction.

The terminal bud in September contains not only the young stem-buds for the next growing season but also two or more young stem-buds for the second season in advance. Usually the first of these stem-buds, which already has cut off the primordia of lateral organs, fails to develop farther. Each stem-bud is formed in the base of a fleshy scale-like body which in turn arises in the axil of a bud-scale or sheath. At least a rudimentary stem-bud is found in the axil of every bud-scale.

The rootstock of *T. sessile* var. *giganteum* bears lateral branches or offsets, which in time become separated by decay of tissue from the parent plant, thereby affording a ready means of vegetative reproduction. Such offsets are rarely found in *T. ovatum*.

2. The active season in *T. sessile* var. *giganteum* lasts from February to July. In the vicinity of San Francisco Bay, however, unfavorable atmospheric and soil conditions cause a majority of plants to end their active season prematurely. On the other hand, in *T. ovatum* the active season is greatly prolonged. The former species ripens its fruit in July, the latter in May.

3. During the active season the young stem-bud, or buds for the next year whose activity had been suspended late in the previous active season, begin to grow anew and differentiate various parts. At the same time additional stem-buds are laid down of which some may develop into buds for the next season. Those laid down last, however, and therefore least differentiated, are checked in May, so that they cannot develop farther until the next active season arrives.

4. In *T. sessile* var. *giganteum* a plate consisting of four rows of archesporial cells is cut off in each locule of the anther in May. Late in August or in September the tapetum is cut off.

5. The dormant season in *T. sessile* var. *giganteum* lasts from August to January inclusive. However, activity is renewed in the underground organs when the rainy season begins, in September or October.

6. The pollen mother-cells divide after the parts of the plant have begun to show renewed activity in growth. If a plant has several stem-buds for next season their pollen mother-cells divide at different times. Other causes affect the time when the meiotic divisions occur, but it may be said that in general the pollen mother-cells of *T. sessile* var. *giganteum* divide in October and November. The various phases of the two divisions, including synapsis, occupy not more than three weeks, and the pollen grains are cutting off generative nuclei in three weeks after the completion of the homotypic division. Mature pollen may be found in November and December. From that time onward no changes are taking place in the anthers except the development of the mechanism of dehiscence. In many pollen mother-cells the nuclei degenerate in synapsis or before, and many pollen grains fail to develop properly. In *T. ovatum* the pollen mother-cells divide in August and September and practically all pollen is mature by November 1.

7. The megaspore mother-cells are differentiated just before the microspore mother-cells divide and change but little in appearance in *T. sessile* var. *giganteum* before the young shoot appears above ground. The megaspore mother-cell divides and the female gametophyte de-

velops while the young shoot is growing most actively. At the time of anthesis the embryo-sac is mature. In *T. ovatum* the large size of the ovules in midwinter and the rapidity with which the plant comes into flower in spring indicate that the megaspore mother-cell divides before the young shoot has appeared above ground.

8. In *Trillium grandiflorum* in the eastern United States and in northern Germany the dormant period is approximately equal in length to the dormant period in *T. sessile* var. *giganteum* in the vicinity of San Francisco Bay. According to Atkinson, in *T. grandiflorum* the pollen mother-cells are cut off and pollen may even be fully matured at the beginning of the dormant period, whereas in *T. sessile* var. *giganteum* pollen mother-cells are cut off within the dormant period. In most plants of *T. grandiflorum,* however, maturation of pollen occurs after the subterranean parts have begun to show indications of renewed growth. The same is true of *T. sessile* var. *giganteum.* In *T. sessile* var. *giganteum,* just as in *T. grandiflorum* and *T. recurvatum,* the megaspore mother-cell divides after the young shoot has appeared above ground. In *T. ovatum,* on the other hand, pollen is usually mature before the close of the prolonged active season, and the megaspore mother-cell is apparently ready to divide two months before the shoot appears above ground.

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VII. Explanation of Plates

PLATE 7

Stem-buds of *Trillium sessile* var. *giganteum* from the rootstock crown in various stages of development. Semi-diagrammatic.

Fig. 1. Longitudinal section of bud collected in November, primordia not all present, still very rudimentary, fifteen months before its active season above ground commences.

Figs. 2 and 5. Bud in February: figure 5, entire, figure 2 in longitudinal section. Primordia more highly differentiated than in November. The sepals slightly surpass the foliage leaves.

Figs. 3 and 6. Bud collected in May: figure 6 entire and figure 3 in longitudinal section. The foliage leaves are seen to be shorter than the sepals. Sepals and petals now include the stamens and carpels. At about this time the archesporial cells are cut off in the young anthers.

Figs. 4 and 7. Bud as it would appear late in July: figure 7 entire and figure 4 in longitudinal section. The foliage leaves are now growing rapidly and equal or slightly surpass the sepals in size. As in figure 3, the maturing anthers practically fill the interior of the flower bud. In *T. ovatum* the flower bud at this season would be elevated in a short peduncle. For comparative sizes of the different parts of the stem-buds in September, see figure 1, page 44, b_2, b_3.

Fig. 8. Portion of cross-section of a young anther showing archesporial cells just cut off. Collected May 29, 1915.

Fig. 9. Portion of young ovule showing the megaspore mother-cell. Collected October 7, 1914.

Fig. 10. First division of megaspore mother-cell. Collected February 26, 1915.

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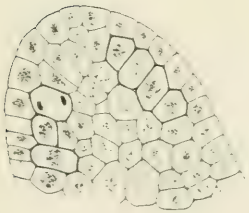

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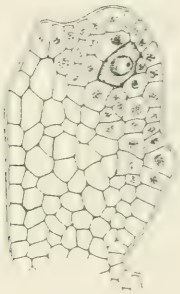

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PLATE 8

Fig. 1. Young pollen mother-cells in the resting condition immediately preceding synapsis.

Fig. 2. Young pollen mother-cells in synaptic condition.

Both conditions were found in different anthers of the same flower bud collected November 26, 1914.

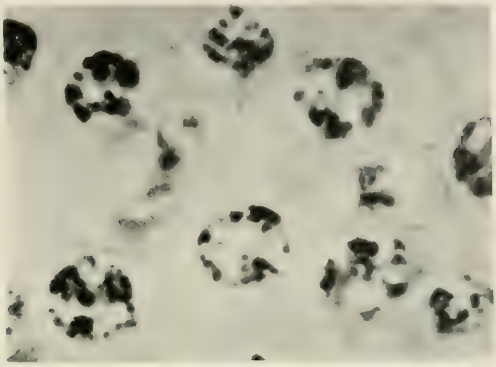

Fig. 1

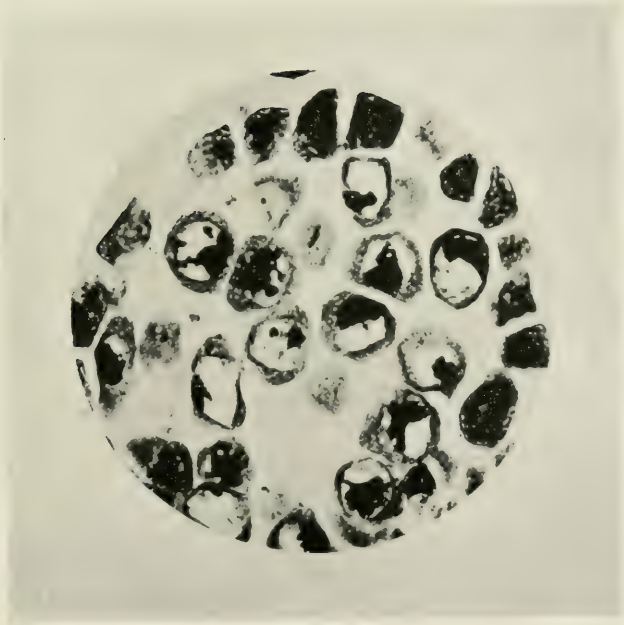

Fig. 2

PLATE 9

Fig. 1. Pollen mother-cells in the metaphase of the heterotypic division, both polar and longitudinal views of the spindle. The reduced number of chromosomes is clearly discernible in at least one of the division figures. Collected October 21, 1914.

Fig. 2. Portion of a mature locule showing parietal tissue and a few mature pollen grains. Collected March 11, 1916.

Fig. 1

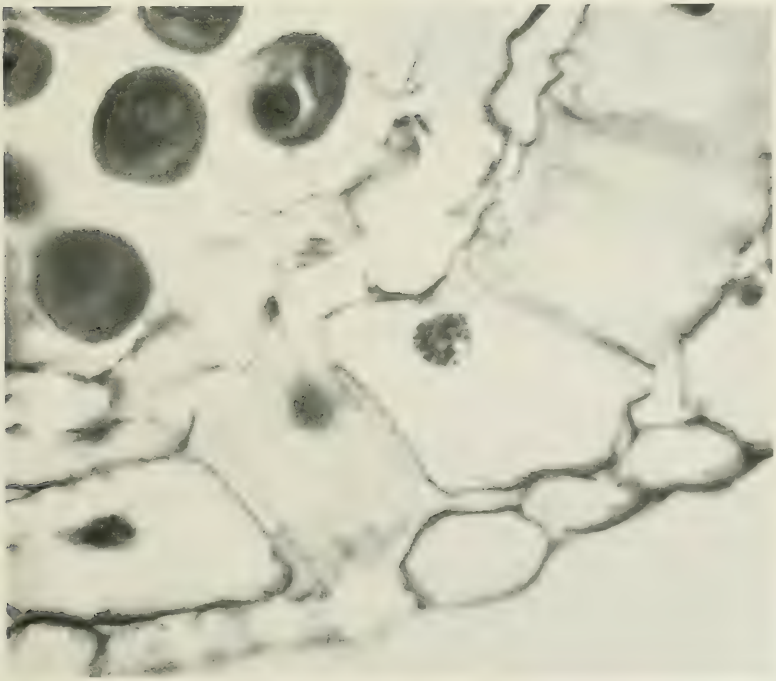

Fig. 2

PLATE 10

Fig. 1. Germination of the microspore. Collected November 5, 1913.

Fig. 2. Adjacent walls of two locules of a mature anther just before dehiscence. A layer of small cells has been formed which cuts across the walls of both locules to assist in effecting dehiscence. Collected March 7, 1915.

Fig. 1

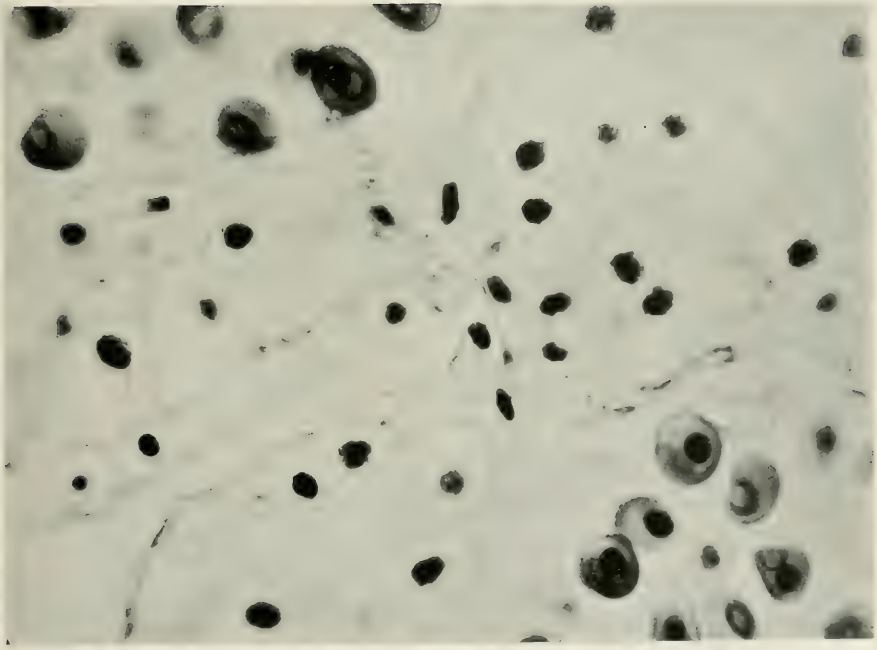

Fig. 2

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NOTES ON THE CALIFORNIAN SPECIES OF TRILLIUM L.

IV—TERATOLOGICAL VARIATIONS OF *TRILLIUM SESSILE* VAR. *GIGANTEUM* H. & A.

BY
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The genus *Trillium* has long been recognized as unusually prone to the production of teratological forms, and the occurrence of such abnormalities has from time to time been noted for practically all the more common and well-defined species. It is the purpose of the present note to gather together a number of the references to teratology in the genus, and particularly to describe the nature of a number of abnormal forms found in the Californian representative of *T. sessile* L.

A rather thorough examination of the available literature has resulted in the accumulation of a considerable number of references to *Trillium* teratology. Since a compilation of the literature on the subject has not, to my knowledge, been attempted, and especially since many observers have published accounts of abnormalities apparently without knowing that similar specimens have a number of times been described elsewhere, it has seemed best to bring together certain of the somewhat scattered references and to arrange them under the species to which they severally refer. No claim is made for the completeness of the list submitted below, since often in the older literature only the briefest notices are given to teratological phenomena. It seems probable, however, that most of the more important contributions have been examined.

Trillium grandiflorum (Michx.) Salisb.

This species appears to be the most highly variable of the nine here noted, as is indicated by the predominating number of references in the literature on teratology in the genus. Britcher (1902) has described at some length the extraordinary series of abnormal forms which occur near Syracuse, New York. He includes measurements of such characters as "length of stem," "length of petiole," "size of leaf blade," "length of peduncle," etc., together with notes upon the more highly abnormal variations observed. Flower color was found to vary for the petals from "typical white or pink, through white with green center stripe, to solid green." The following is Britcher's condensed tabulation of the measurements on variation in size of parts (*loc. cit.*, p. 196):

Length of plant stem varies from	0 mm.	to 340 mm.
Length of petiole	0	160
Width of leaf blade	22	124
Length of leaf blade	30	157
Length of peduncle	2	220
Length of sepal stem	0	44
Width of sepal blade	9	37
Length of sepal blade	26	78
Length of petal stem	0	64
Width of petal blade	8	50
Length of petal blade	18	80
Length of filament	1	34
Length of ovary	1	30
Length of ovary stalk	0	23
Length of style	2	27
Length of anther	0	20

Atkinson (1905) notes two teratological modifications. In the first case the flower shows the "compound pistil expanded into three leaf-like members." This in general corresponds to Britcher's plant 128: "The place of the ovary is taken by three leaflike parts with stems 10 mm. and blades 5 by 14 mm. in size. Within this circle are two pollen-bearing stamens with filaments 4 and 7 mm. long and anthers 5 and 10 mm. long" (p. 174). Atkinson's second abnormality is not noted by Britcher, who does not definitely describe any instance in which all the parts of the perianth are strictly foliaceous or in which a duplication of parts occurs. In this second case "the nine parts of the perianth are green and the outer whorls of stamens are expanded into petal-like members." From the illustration there is obviously an extra whorl of perianth segments; the outer whorl of expanded

stamens are anther-bearing along their margins, while the inner whorl of stamens and the pistil are normal.

Bishop (1902) gives cases included under Britcher's plant 103 (p. 178) and others in which the peduncle is longer than the stem below the leaves. He refers to other cases showing an extreme length of petiole (Britcher's plant 109, and others, p. 189), and states: "The green-petalled variety is common . . . Multiplication of organs is common, in one case extending not only to the petaloid and bractlike forms, but also to the leaves." Davis (1897) reports the examination of a large number of abnormal specimens, among which "the simplest departure was markedly the presence of green stripes in the petals," adding that "this striping was accompanied by a lengthening of the petioles and degeneration of the pistil." He found over fifty individuals in which the leaves were reduced to bracts or had entirely disappeared (cf. Britcher, plant 149*a*, p. 174) and notes that "in such forms the stamens are the most stable of the organs of the flower, only a few reversions to the leaf type occurring, while the pistil was usually sterile, rarely containing ovules, frequently being reduced to the leaf form and sometimes containing well-marked whorls of leaves." Dickson (1897) describes, from Hamilton, Canada, a long-petioled specimen corresponding to a number of the plants described and figured by Britcher (cf. p. 189). Dudley (1886, p. 99) speaks of "double-flowered specimens" that "have about fourteen parts to the perianth." Gary (1905) describes the long-petioled and green-flowered forms noted by Britcher and mentions a plant tetramerous throughout. Mrs. Goodrich (cf. *Meehans' Monthly*, vol. 8, p. 182, 1897) reports the common variations found by Britcher from the same locality in which his collections were made.

Gray (1875*a*) mentions a long-petioled form with green, striped petals and a plant with similar petals, no leaves and having sepals which were "more foliaceous than is usual and are fully two inches long, quite equalling the petals." These plants were from St. Louis, Michigan, and compare to individuals found later by Britcher. Gray (1875*b*) notes still other forms described by Britcher and says that they suggest large specimens of *T. nivale* because of their long-petioled leaves, but that they are sharply distinguished from this latter species by "the acute base and acuminate apex of every leaf." Hankensen (1870) describes plants of the Syracuse type from Newark, New York, and lays emphasis upon the fact that plants without leaves apparently have larger, foliaceous sepals. In this connection, attention might be

called to an observation by Peck (1885) who, in describing the usual long-petioled, green-striped variation, says that "the specimens indicate a coincidence between the petioles, peduncles and green color of petals. Generally the longer petioles are accompanied by longer peduncles and broader green stripes on the petals. The coincidence between form and structure is truly remarkable."

Holzinger (1901) figures a plant in which the leaves are normal but the flower consists of six whorls of three green, foliaceous perianth segments each. Osband (1894) describes an unusual plant, the flower of which exhibited two whorls of three normal sepals each; similarly two whorls of petals, the outermost being striped or white; and three stamens, of which only one was normal, one being "expanded into a half-sized petal" and anther-bearing, and the third sterile. The ovary is reported as normal in size but "near the top of one of the carpels arises an outgrowth about half an inch long, white, doubled together and drawn over at the top like a hood." On the edges of this outgrowth there were "two pollen-bearing lines about an eighth of an inch long."

Pollard (1901) reprints the figure and description of a plant noted by Mrs. Kellerman (1893). The plant bore a conspicuous double flower, and the double condition reappeared for some years from the original rootstock, which was brought into a garden. The flowers were white in color and varied in number of whorls of petals from nine to thirteen. The reproductive tissues were almost completely suppressed. Smith (1879) comments upon the number of abnormal individuals and their wide distribution in Michigan. Nothing is added to the types noted by Britcher, but the statement is made that in abnormal plants "the ovules are sometimes twelve in number, but generally less, often none, or only one or two, the cavity being filled by an enlarged placenta." It might be mentioned in this connection that rootstocks of normally fruiting plants of *Trillium sessile* var. *giganteum* H. & A. when brought under greenhouse conditions have apparently no dormant period (cf. Brandt, 1916), and each of the flowering shoots matures a large ovary which contains only a spongy mass of placental tissue. With regard to the prevalence of abnormal individuals in Michigan, Meehan (1894*b*) reports that many plants are found with "four leaves, three sepals, and four petals, a less number with four leaves, three sepals, and five petals." Since these forms are found only at the end of the season, a causal relation is suggested between lateness of flowering and abnormal variation.

Stevens (1894) notes the case of a flower in which "a stamen and a petal were united edge to edge, one anther cell being obliterated by the union." The plant was otherwise normal. Victorin (1904) describes two plants apparently tetramerous throughout. In one flower a petal was anther-bearing. A flower, presumably of *T. grandiflorum*, is mentioned by Meehan (1894*a*) consisting of "eighteen beautiful white petals." A normal whorl of leaves is spoken of and it is probable that the sepals were also normal (cf. Meehan, 1894*b*, who describes a "very perfect eighteen-petalled flower"). The rootstock apparently produced abnormally flowering shoots for three years after being transplanted into a garden. Peck (1888) notes two plants in which "not only petals but also sepals were wholly white."

Trillium erectum L.

Andrews (1906) briefly mentions an abnormal individual of this species, the flower of which showed five petals, four stamens, and two styles, while the outer whorls were normal. Deane (1910) notes a plant with a single whorl of four leaves, five sepals partially petaloid, four petals, eight stamens, one of which was double, and an eight-winged ovary. Bishop (1902) refers to "a few instances where the whorls are repeated but none with the lengthening of leaf and flower stems" so characteristic of the extreme variations of *T. grandiflorum*. Clute (1895) reports a flower of this species with four petals—each edged by a pollen-bearing anther—and five stamens. James (1884) describes a teratological specimen of the following type: four sepals, four petals, eight stamens, "four pistils and a four-celled ovary," whorl of leaves normal, a fourth leaf on the peduncle halfway between flower and leaves, and the sepals wholly or partially petaloïd.

The remainder of the pertinent references to *T. erectum* which have been found deal with the color of the flower and especially the occurrence and origin of the var. *album* Pursh. Gray (1908, p. 293) describes the petal color of *erectum* as "brown-purple, or often white or greenish or pinkish." Thus a considerable range of color-forms seems well recognized. Hall (1870*a*) comments upon the occurrence of the normal "purple" form associated with the less strongly pigmented forms. He says: "I have watched individual plants of this variety (var. *album*) as closely as possible, and seen the regular purple flower in their place the next year; and have also seen the var. *album* flower in places when the year before a purple flower had appeared. I have noticed, too, that, as a rule, the var. *album* is a starveling;

rarely as large or as healthy as the purple plants in the midst of which it grows. Also I have rarely found a var. *album* away from the company of the normal plant, and never more than three or four plants together, though they are quite common." Elsewhere (1870*b*) he notes the occurrence of a plant with "creamy green" colored petals for a number of years after being transplanted to a garden. Gary (1905) mentions a plant with cream-colored petals and red ovary, and Horsford (1890) reports a considerable local variation in the color forms of this species. Thus, from Pennsylvania comes "the true var. *album* with pure white flowers as white as those of *T. grandiflorum*. Indeed, a casual observer would take them for *grandiflorum*." A shade intermediate between the "pure white and the typical *T. erectum*" and a form in which the "petals are of a yellowish shade with a sprinkling of purple" are found in Connecticut. "Both forms of the variety and the true purple type" occur together. Clute (1908) gives some evidence in this connection. He says that "in eastern America it is almost invariably dark purplish red in color; in the west it is invariably pure white without even a tinge of red." Plants of the red form sent to him from New Britain, Connecticut, came up in his garden (Joliet, Illinois) the following spring bearing, with one exception, pure white flowers, and in this one instance there was only a "trace of red in the stamens." I have been unable to learn more as to the later history of these plants. Clute (1907) also describes a "yellow trillium" in which the "inner three leaves of the perianth were wholly a pure sulphur yellow; the outer leaves of the perianth were pale green below, but as bright a yellow above as the inner part of the perianth." The species is not noted, but the statement is made that the plant "grew amongst a larger number of specimens of *T. grandiflorum*." The remark is made that "seeds from an aberrant plant will usually produce the same form." In seeking an explanation of the origin of var. *album*, it seems possible that in general it may represent a type of "undeveloped flower" such as is common in the sessile-flowered Californian species (cf. Goodspeed and Brandt, 1916*b*), although the occurrence of intermediate shades between white and red might rather be taken to preclude such an interpretation. Certainly controlled breeding experiments are very necessary in this connection.

Strictly teratological variations in *erectum* seem to consist solely of various degrees of doubling without accompanying malformations of a striking character.

Trillium sessile L.

Andrews (1906) describes two abnormal plants of this species. One bore fourteen "floral leaves," and it was noted that "no trace of the usual stamens or pistil was present, all the floral organs being completely transformed into floral leaves." The other plant had four leaves, three (?) sepals, "four large partly-greenish petals, six small stamens and four styles." Foerste (1891 and 1894) in two articles discusses the phylotaxy of a number of teratological individuals, describes the effort of the typically trimerous plant to accommodate itself to the dimerous conditions, and comments upon the ability of one abnormal individual to maintain the quaternate arrangement with only six floral envelopes. He mentions five cases of doubling in this species. One plant was four-parted throughout, the whorls being normally oriented. A second plant bore four leaves, two sepals, four petals, two of which were partially sepaloid, and six stamens. Another plant is described as being four-parted, except that one petal is missing and but six stamens (all double) are present. A fourth plant was more highly abnormal and irregular, bearing five leaves, two sepals, three petals, seven stamens, and a four-celled ovary. Hopkins (1902) describes three teratological shoots, all from the same rootstock. One showed three whorls of three leaves each, four petals, no sepals, five stamens, three styles and stigmas, and the ovary six-angled; another, two whorls of three leaves each, no sepals, six petals, seven stamens, four styles and stigmas, and the ovary eight-angled; while the third corresponded to this last, except that nine stamens were present and there were but two styles and stigmas. The author assigns the condition of this teratological individual to over-nutrition. Morris (1902) notes the fact that the production of single, long-petioled leaves from the rootstock has been widely mentioned in general descriptions of the genus. He describes and figures a rootstock of *sessile* which bears two normal, flowering shoots from the terminal rootstock crown and in addition two small lateral offsets, each bearing a single one of these long-petioled leaves. As stated by the author, "these leaves sprang, each from the node nearest the apices of two tiny branches from the main rootstock." Hankensen (*loc. cit.*) also mentions plants of *grandiflorum* with a single radical leaf.

This question of the production of single, long-petioled leaves from the rootstock of *Trillium* is one which has throughout been of considerable interest in our studies upon the Californian species. As

elsewhere noted in this series of papers, the quite characteristic sterility of var. *giganteum* seems to be compensated for by very active vegetative reproduction by offsets of the rootstock. In this connection it may be recalled that *ovatum*, a heavily fruiting species, practically never reproduces vegetatively. A single rootstock of *T. sessile* var. *giganteum* may exhibit from three to six normally flowering or normal flowerless shoots from the rootstock crown and an equal number of offsets of varying ages which may bear either a single, simple, long-petioled leaf, or a small but normally three-parted whorl of leaves, or, more rarely, two opposite leaves. Plate 11 shows two rootstocks, one of which bears a two-leaved shoot from the crown, and the other a single, long-petioled leaf from the same position on the rootstock and in addition a similar leaf from an offset. These forms occur very commonly in California, and the problems connected with their origin and the mode of transition from the simple one-leaved to the three-leaved condition are being investigated in connection with those brought up by the occurrence of undeveloped flowers.

Trillium undulatum Willd.

Beattie (1905, p. 40) comments upon the large proportion of two-stemmed plants of this species in Rhode Island and notes an instance of phyllody in one shoot of a two-stemmed individual, while the other shoot apparently was entirely normal. Peck (1878) describes from Oswego, New York, a plant in which there was almost perfect doubling of the number of parts in whorls of leaves and flower parts.

Deane (1908*a*, *b*, and 1910) describes a number of interesting teratological specimens and gives important evidence as to the recurrence of such variations in succeeding years. Three abnormal forms in the Gray Herbarium are described. The first was apparently normal except that the sepals were greatly enlarged and foliaceous, somewhat corresponding to the forms noted by Beattie (*loc. cit.*), and the second was octamerous throughout except that there were seven stamens. Deane re-examined the "polymerous" specimen described by Gray (1878) and found it to consist of eight sepals, one with a "white petaloid growth on one side," eight petals, "at least twenty stamens," six carpellary divisions of the ovary, and seven leaves, one of which was double. Another plant is described from Maine which bore four leaves, three sepals, three petals, six stamens, one more or less petaloid, and a one-celled ovary. All parts were normal in shape

and size. Of special interest is the description of the recurrence during two seasons, following the one during which the plants came under observation, of a group of teratological individuals. In general, the plants strikingly resembled the remarkable specimens of *sessile* described by Hopkins (*loc. cit.*). The station is Squam Lake, Holderness, New Hampshire, and there seems to be no doubt but that corresponding abnormal variations were produced by the same rootstock or rootstocks over a period of three seasons.

Trillium cernuum L.

I have found but two references to teratology in this species. Owen (1894) describes two specimens from New Hampshire. One showed a normal whorl of three leaves and above it "three whorls of three leaves each," the sepals larger than common, petals with a white stripe running down the center and a green stripe on each edge and one of them two-parted, four stigmas. The other specimen exhibited a "rosette of two whorls, a third abnormal in this specimen also, but lifted one-half inch above the others to the base of the flower." Tracy gives the following description of an abnormal individual: "One petal and two sepals of the ordinary form and color, while the third sepal has been replaced by a perfect leaf, and the other two petals have a green stripe through the center."

Trillium nivale Riddell.

Andrews (1906) reports that in this species "some slight deviations have been observed . . . in the way of a union of the floral parts."

Trillium recurvatum Beck.

Andrews (*loc. cit.*) notes a plant with twenty-three "floral leaves" in which no trace of the "usual stamens or pistil was present, all the floral organs being completely transformed into floral leaves which were considerably larger (with the exception of the central ones) than the same parts in normal flowers growing near them."

Trillium ovatum Pursh. and **T. sessile** var. **giganteum** H. & A.

In these two western species teratological variations have on only two occasions been described, so far as I have been able to determine. In thousands of specimens of *T. ovatum* which have come under observation in our studies, no abnormalities have been found. Deane (1911), however, describes an interesting plant from Lake Cushman,

Washington. The three leaves are normal but there are twenty-four "petals," eighteen of them in "regular alternating whorls of three, the first, third, and fifth, and the second, fourth, and sixth whorls being superposed upon each other," while "the six petals in the center of the flower form a partially closed cluster." The largest of the six "petals" was 1.8 cm. in length and much "crumpled."

In *T. sessile* var. *giganteum* we have noted a considerable number of teratological variations, the following description of which, with notes on their recurrence from the rootstock, represents the principal purpose of this paper. Miss Eastwood (1896) has given the only description with which I am acquainted, of abnormalities in this western ally of *T. sessile* L. She reports on "three abnormal specimens of white-flowered *Trillium sessile* var. *Californicum* found in the San Bruno Hills of San Mateo County." The first specimen was four-parted throughout, "even the ovary," and the stamens were eight in number. The second bore six leaves, six outer divisions of the perianth and five inner, ten stamens, and a six-celled ovary. The third was normal except that "one of the outer divisions of the perianth was a true leaf." She states that "this species is exceedingly variable in the color, shape and size of its flowers; but such abnormal forms are rare."

I wish in what follows to describe the abnormal shoots produced by seventeen different rootstocks of *T. sessile* var. *giganteum*. Of these seventeen rootstocks, twelve have been or are at present under observation in garden cultures.

1. Collected in Berkeley Hills, Berkeley, California, by Dr. R. P. Brandt; rootstock not preserved. One shoot normal in every respect except the condition of the stamens. These were six in number, but each was flattened and the connective expanded to form structures very similar in appearance to a corresponding condition in *T. grandiflorum* described and figured by Atkinson (*loc. cit.*). In size the individual stamens varied from 32×5 mm. to 32×8 mm., the width measurement being taken across the widest portion of the expanded stamen. Anther cells containing apparently normally matured pollen were present on both edges of each stamen. Partial pistillody of all the stamens also occurred here, in that ridges of lighter-colored tissue stood out from the inner surfaces of the expanded connective and this expanded connective was inflated to a considerable degree. These ridges of tissue undoubtedly represent stylar and stigmatic surfaces, although their likeness to such structures of the pistil is not as

striking as is the case of pistollody of the perianth shown in plate 15, figure 1. No trace of ovules was to be found in the inflated regions of the expanded connective.

2. Collected as 1; rootstock not preserved. Normal in every way except that one petal was much curved and bore a shrunken and empty anther cell along half its inner, curved edge.

3. Collected in the Berkeley Hills; the rootstock not preserved. This plant showed four leaves, averaging 103 mm. in length and 95 mm. in greatest width; four sepals, averaging 46×13 mm.; four petals, of which three were normal and averaged 65×16 mm., and the fourth was curved and anther-bearing as in number 1 above; seven stamens, and four styles and stigmas. The leaves and flower parts were regular and, as indicated, the flower was practically symmetrical.

4. First collected in the Berkeley Hills by Dr. Brandt in 1915, marked and collected again in 1916; the rootstock not preserved. In 1915 this rootstock bore at least two shoots. When this plant was first noted a large collection of mature ovules was being made for cytological purposes; and when the pistils of the shoots from this rootstock were cut open, supernumerary pistils were found within the ovary at the base. This condition was apparently characteristic of the pistils of all the shoots from this rootstock, and the structures themselves, in the case of two of the shoots, were preserved in fluid. One of these intracarpellary pistils is shown in plate 17, *d*. The size of the main carpellary structure was not perceptibly increased and it was normally provided with ovules on parietal placentae while the small included pistils of the type shown in the figure occurred at the base, imbedded in a mass of spongy proliferations of the placental tissue. As will be seen, ovules were present on these intracarpellary pistils, although borne on their surfaces, while the tissues of the ovary within were undifferentiated.

Plants from this rootstock collected the following season (1916) showed merely a trace of the same condition, but distinctly enough to indicate that it is subject to recurrence from this rootstock.

5. Collected in the Berkeley Hills, 1914; rootstock not preserved. Numbers 5 and 6 represent nearly identical instances of pistillody in which the petals are ovule-bearing. Number 5 has been elsewhere described (Goodspeed, 1916) and the nature of the abnormal condition is shown in plate 15, figure 2, and in plate 17, *a*. The description given in the case of number 6 below will, with modification there noted, hold for this plant also.

6. Collected in Marin County, 1916; rootstock in pot 46 of the *Trillium* cultures in the University of California Botanical Garden. This rootstock bore two flowering shoots, one of which was normal in every respect; the condition of the other is shown in plate 15, figure 1. As will be noted, the leaves were normal in number and they were also normal as to shape and size, while the three sepals were partially petaloid. There were six stamens, all normally provided with the long filaments characteristic of plants from this locality. The pistil was also normally formed and ovule-bearing. The striking teratological condition is seen in the petals. They were reduced below the sepals in size, and along their rolled edges ovules were borne, while modified stylar and stigmatic tissue was present along the inner surfaces. The petals of number 5 above were identical except that no trace of stylar and stigmatic tissue was found. The cross-section of the modified petal of number 5 shown in plate 17, *a*, is applicable as descriptive of the condition found here (cf. Halsted, 1891).

7. Collected in the Berkeley Hills by Dr. Brandt and Professor R. R. Gates, 1916; rootstock in pot 40. This rootstock bore six shoots, two of which were entirely normal and four exhibited abnormal modifications in the way of a distinctly fasciated condition and a more or less corresponding increase in number of parts in each whorl in all but one case.

In all four abnormal shoots, the stem was quite strongly flattened and often distinctly ridged. In one case a small sixth leaf was inserted below the main whorl of five leaves and from it a ridge or petiole ran down the entire length of the stem.

Two shoots bore five leaves, four sepals, four petals, eight stamens, and from four to six styles and stigmas, while the ovary was usually composed of one large cell with from six to eight parietal placentae. A third abnormal shoot was similar with the exception of the presence of a sixth leaf noted above. There were various more or less unimportant modifications of organs, such as the union of two stamens, a partially petaloid stamen, a petal curved and anther-bearing along one edge. In one case there appeared to be two distinct whorls of leaves distinguished by size as well as height of insertion. One of these three shoots is figured in plate 14, figure 2, and the nature of the pistils is shown in plate 17, *b* and *c*.

The fourth abnormal shoot of this rootstock is figured in plate 13. At the top, along the ridge formed by the much-flattened stem, fourteen leaves were borne, and just below a complete three-

parted whorl of leaves corresponding in shape and provided with a small undeveloped flower in the center (cf. Goodspeed and Brandt, 1916*b*). Within the leaves on the ridge at the top of the stem were a series of five such undeveloped flowers. The leaf measurements show that there were five distinctly larger leaves, and these made up a somewhat irregular outer whorl. Some years ago another plant of almost exactly this description was found in the Berkeley Hills, but the rootstock unfortunately was not kept under observation.

8. Collected in the Berkeley Hills, 1916, by Dr. Brandt; rootstock in pot 47. This rootstock produced six flowering shoots, five of which were normal throughout. The sixth was again a fasciated shoot with flattened stem bearing two whorls of three leaves each, the leaves of the outer whorl being somewhat the larger. There were also four sepals, all of them foliaceous; five petals, nine stamens, three long and six short; six styles and stigmas, and a single large-celled ovary with six parietal placentae.

9. Collected in Marin County, 1916; rootstock in pot 41. This plant is figured in plate 12. As will be seen, the rootstock produced two shoots, both of which bore a single four-parted whorl of leaves with an undeveloped flower. The other shoot is arranged on the plan of 5, with ten stamens and a one-celled ovary with five placental surfaces.

10. Collected in Marin County, 1916; rootstock in pot 45. This rather unusual individual is shown in plate 14, figure 1. Its striking abnormality consists in the condition of the sepals, which are reduced to shriveled, scalelike structures. The petals were, also, of a peculiar shade of yellowish-green, very brilliantly shining, while the ovary was white and the stamens light violet in color.

The following individuals have been under observation for a year or longer in the garden cultures:

11. Collected in Marin County, 1911; under observation for five years:

1911—Rootstock collected with two entirely normal flowering shoots.

1912—Two shoots produced. One shoot entirely normal and the other bearing four leaves, three sepals, four petals, and six stamens, one of which was connected with a petal.

1913 to 1916—One or two entirely normal shoots produced each year.

12. Rootstock collected in 1911; until 1916 produced two normal shoots each year with undeveloped flowers. In 1916 there appeared three very small shoots, one of which bore four leaves and an undeveloped flower, while the other two shoots were normal.

13. Collected in 1910; until 1914 produced normal shoots. In 1914 the two shoots figured in plate 16, figure 2, both bore large undeveloped flowers. On the shoot shown in the right in the figure, one leaf was diminutive in size, thin and transparent, and rather tightly curled about the flower. It was, further, inserted within the leaf whorl. In the figure it is shown partially folded back to display the flower. In the two following seasons the shoots from this rootstock were entirely normal.

14. Collected in Marin County in 1911, this rootstock had produced five offsets, which were separated from the parent rootstock and planted in separate pots. The parent and the offset rootstocks have since that time borne normal shoots with the exception of one of the offsets, which in 1912 produced the two shoots seen in plate 16, figure 1. Since 1912 this rootstock has given rise to normal plants.

15. When collected in the Berkeley Hills in 1912, this rootstock bore two shoots—one normal and in flower, and the other with a flattened stem, six leaves, and a small undeveloped flower. In 1913 and 1914 two normally formed whorls of leaves were borne with undeveloped flowers. No shoots were produced thereafter.

16. Collected by Dr. Brandt in 1915; rootstock in pot 149. There is no record as to place of collection or as to condition of plant, except that it was highly abnormal. In 1916 this rootstock produced one shoot with three leaves, three large foliaceous sepals, five petals, and three stamens. One stamen was normal in shape and size, but was strongly bent inward for a distance of 3 mm. below the tip. Another stamen was petaloid and anther-bearing along only one edge, and the third was distinctly double.

17. Collected in 1915; rootstock in pot 150. Again there is no record except that the plant was abnormal in number of parts. In 1916 this rootstock produced six shoots. Two of them were normally flowering; two were likewise normal, but provided with undeveloped flowers; one bore four leaves, and the sixth seven leaves, with undeveloped flowers in both cases.

DISCUSSION

There seems to be little doubt that within the Eastern species *grandiflorum* there is a widely distributed form or variety which exhibits correspondingly rather marked variations in the various localities from which it has been reported. This form, sometimes referred to as var. *variegatum* Pk. (cf. Peck, 1888), is characterized by long-petioled leaves, striped perianth segments, and often an elongation of the peduncle. Apparently no other American species possesses any similarly well-marked and widely distributed form or variety based upon abnormal structural variations. Color variations in most of the species are striking and well recognized but probably represent, with possibly one or two exceptions, extremes of the normal fluctuating variation of a highly variable genus. Although var. *giganteum* contains no characteristic form of extreme or teratological structural variation, the extent and intensity of such variation seems remarkable. That practically all organs of the flower may exhibit duplication of parts, suppression or extreme modification and metamorphosis, has been indicated in the description of specimens above.

The question of the recurrence from the rootstock and, in the case of perennial plants in general, of abnormal shoots, and the more important question as to the origin of such inherently abnormal rootstocks, are of maximum interest and significance. The genus *Trillium* would seem to furnish rather unusually valuable and readily investigated material for such studies. As yet, however, the evidence at hand, if not contradictory, is at least highly fragmentary and in general rather unsatisfactory so far as this genus is concerned. The observations on Eastern species, especially those of Deane on *undulatum*, indicate that, in the case of well-defined and extensive teratological variation, the abnormal condition may be expected to recur year after year in the shoots produced by a given, inherently abnormal rootstock. Our garden cultures of var. *giganteum* seem to suggest much the same condition, although the more important evidence will come from the results of the next few years. There is no doubt, however, that such apparently relatively simple variations in structure as the change from the trimerous to the tetramerous condition do not recur in succeeding years from the same rootstock. Our cultures appear to indicate that such changes may be environmentally determined, a fact further suggested by the ease with which many of the

most fundamental ontogenetic processes of the plant can be modified by cultural influences. Field studies and garden cultures, however, do not support the suggestion, elsewhere noted, that these transitory or the other more deeply seated teratological variations are connected with the time of appearance of the shoot during the growing season.

An inherently abnormal rootstock, which may be expected always to produce some abnormal shoots each season, must have had its origin in a seed, since there is no evidence, on the one hand, that variations induced in rootstocks by environmental conditions will recur or, on the other, that the individuals produced by offsets (asexual reproduction) differ in any way from the shoots formed from the parent rootstock. This latter point has been thoroughly investigated in seeking an explanation for the origin of the remarkable range of color forms found in var. *giganteum*. It is unfortunate that no one has grown the progeny of a teratological individual. It is apparent that among the Eastern species certain of the abnormal individuals observed do produce a little seed, and this is, I judge, especially true of *T. grandiflorum* var. *variegatum*. It is highly desirable that someone determine the proportional occurrence of the variety and the normal form from the seed of var. *variegatum*. Unfortunately var. *giganteum*, even in the case of entirely normal flowers, only rarely produces viable seed, and thus it is probable that only the question of the recurrence of teratological variations from the rootstock can be investigated.

In general the initial production of the seeds giving rise to teratological rootstocks can apparently be explained most readily on the assumption that the parent plant was in a basically heterozygous condition. The occurrence of abnormalities following hybridization, especially in the case of wide crosses, is well recognized. A case somewhat in point is that of species hybridization in the genus *Nicotiana*, in which the back-cross *N. sylvestris* × the F_1 hybrid *N. tabacum* var. *macrophylla* × *N. sylvestris* yields a rather high percentage of very abnormal individuals. In this connection it might be noted that the wide range of color forms in *T. sessile* var. *giganteum* seems best explained on the assumption of initial crossing of widely differing forms, an assumption perhaps borne out by the rather widespread sterility in this variety. Finally, it should be borne in mind in connection with this latter point that *T. ovatum*, which exhibits a relatively narrow range of variability in flower color and in form and size characters and rarely gives rise to teratological individuals, produces an abundance of viable seed.

SUMMARY

1. An effort has been made to tabulate the more important references in the literature to teratological variations found in the following species of *Trillium: grandiflorum, erectum, sessile, undulatum, cernuum, nivale, recurvatum, ovatum*, and *sessile* var. *giganteum*.

2. Seventeen teratological variations of *T. sessile* var. *giganteum* are described.

3. Evidence is given to show that such relatively superficial variations as the change from the trimerous to the tetramerous condition do not recur in succeeding years from the same rootstock, while more profound structural variations may so recur.

4. It is suggested that the origin of such recurring teratological variations may be due to the heterozygous condition of an original parent plant.

Transmitted September 8, 1916.

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PLATE 11

Entire plants of *Trillium sessile* var. *gigauteum*, showing single and two-leaved conditions.

PLATE 12

Two abnormal shoots and the rootstock described under 9, on page 81.

PLATE 13

One of the abnormal shoots of the rootstock described under 7 on page 80.

PLATE 14

Fig. 1. One of the abnormal shoots of the rootstock described under 10 on page 81.

Fig. 2. Abnormal shoot of the rootstock described under 7 on page 80.

PLATE 15

Fig. 1. Abnormal flower of the shoot from the rootstock described under 6 on page 80.

Fig. 2. The same type of flower of the shoot from the rootstock described under 5 on page 79.

Fig. 1

Fig. 2

PLATE 16

Fig. 1. One normal and one abnormal shoot from the rootstock described under 14 on page 82.

Fig. 2. One normal and one abnormal shoot from the rootstock described under 11 on page 81.

Fig. 1

Fig. 2

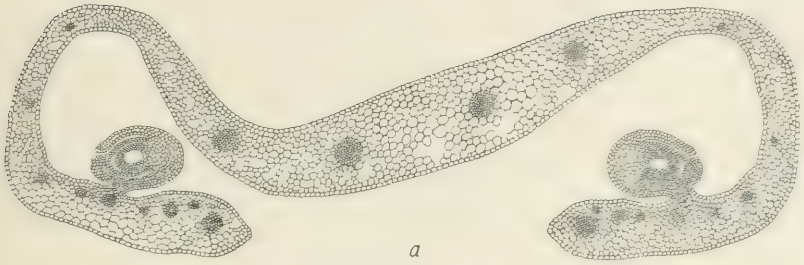
PLATE 17

a. A cross-section of an ovule-bearing petal described under rootstocks 5 and 6 on pages 79 and 80.

b. View of the abnormal pistil and increased number of stamens characteristic of the abnormal shoots of the rootstock described under 7 on page 80. × 2.

c. Pistil of one of these same abnormal shoots showing the ovary opened longitudinally. × 2.

d. One of the intracarpellary pistils of the flower from the rootstock described under 4 on page 79. × 8.



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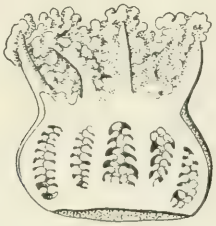

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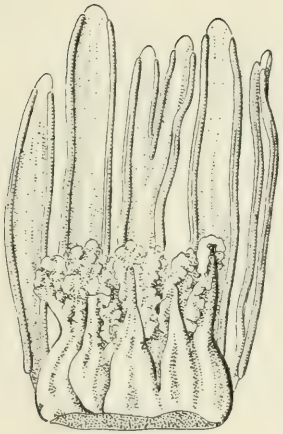

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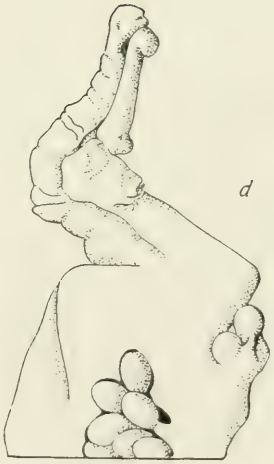

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A PRELIMINARY LIST OF THE UREDINALES OF CALIFORNIA

BY
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I. INTRODUCTORY STATEMENT

The study of the *Uredinales* of California began with the pioneer work of Dr. H. W. Harkness and Justian P. Moore, who in 1880 published a *Catalogue of Pacific Coast Fungi,* which enumerates fifty-five species belonging to this group. Unfortunately this list does not give the specific names of a large number of the host plants referred to and also the localities are often very indefinite, which makes it difficult to correlate this list with the work of subsequent collectors. Somewhat later Dr. Harkness, either in conjunction with M. C. Cooke and J. B. Ellis, or independently, published in *Grevillea* and in the *Bulletin of the California Academy of Sciences* a number of new species including many Uredinales. The extensive collections of Pacific Coast fungi which Dr. Harkness had presented to the California Academy of Sciences before his death were destroyed in the great fire of 1906, with the exception of the types of new species discovered by him, which fortunately were preserved through the foresight of Miss Alice Eastwood, the present Curator of the Herbarium.

In 1882 Mr. E. W. D. Holway began work on the rust flora of California by an extended exploration of King's River Cañon and vicinity, which brought to light a large number of species, some of which were published as new by Dietel and Holway, especially in *Erythea* and *Hedwigia*. With the aid of Mr. Holway this work was continued by the writer, and collections were made in the region about San Francisco Bay (1893 and later), Shasta and Siskyou counties (1894), Tuolumne and Calaveras counties (1895), Lake Tahoe (1897), and Mendocino and Humboldt counties (1896 and 1899). Contemporaneously and in the succeeding years a large number of collectors did work in other regions. Of these especial mention should be made of A. J. McClatchie (Pasadena), S. B. Parish (San Bernardino), J. Burtt Davy (Berkeley), W. R. Dudley, and C. H. Thompson (Stanford University). In more recent years extensive collections have been made by Ellsworth Bethel, Carl T. Baker, David Griffiths, E. E. Heller, Dr. Meinicke of the Federal Forest Service, and Professor Horne of the Agricultural Experiment Station of the University of California.

II. THE NEED OF EXPERIMENTAL CULTURE WORK

Although much more extended collections and critical studies in both field and laboratory must be made before our knowledge of the California representatives of this group of fungi can be considered either exact or complete, it is believed that an attempt to summarize the information now available will be of assistance to those working on the rust flora of the state and will give at least an approximate idea of its extent and content. The need of systematic culture experiments designed to establish with certainty the life histories of those species which are known to be heteroecious is a pressing one. The results obtained in other regions of the United States, especially by Arthur and his collaborators at Purdue University, suggest the species of host plants probably concerned in the life histories of many of the Pacific Coast species; but the differences in the climatic conditions of the two regions and of the species of host plants found in them make it extremely desirable to confirm these suggestions by actual experiments. It is to be regretted that owing largely to the lack of such data it has been found necessary to include in the list here presented a considerable number of form species, that is, aecial and uredineal forms not definitely correlated with the mature forms

necessary for their identification. Apparently an unusually large number of Pacific Coast forms winter over, by means of uredineal spores, and produce telia only occasionally and in very small amounts or fail entirely to do so.

Culture experiments are also greatly needed for the purpose of ascertaining the specific identity of many of those species which develop on closely related host plants, such, for instance, as the forms of *Puccinia* which are found on the different genera of the *Onagraceae* and *Compositae*. Such experiments in other regions have shown great variability as to the closeness of the adaptation between the rust and its host. In some instances, as illustrated by the classical work of Eriksson and Hennings with the grain rusts, this relation is an extremely narrow one and it becomes clearly necessary to recognize species or subspecies based upon purely physiological distinctions. It has been shown by Bethel, on the other hand, that certain species, such as *Puccinia subnitens* and *P. stipae*, produce their aecia on hosts belonging to genera representing widely different natural families, and it is not improbable that too much emphasis has been placed upon the host plant as a criterion in ascertaining the specific limitations of the rusts.

III. PLAN OF THE PRESENT PAPER

As one of the chief objects of the present publication is to assist collectors in naming new collections and to tabulate all the known forms and their accompanying host plants, the different genera, which can usually be readily recognized if the mature form is at hand, have been arranged alphabetically, and where a large number of species are represented those species which occur on host plants belonging to the same natural family have been grouped together and the groups arranged according to the sequence of families found in Jepson's *Flora of Middle Western California*.

The references cited are designed merely to identify with certainty the form referred to and to indicate where a description of it can be found. Only those synonyms have been given which are necessary to show where certain species, whose validity is not accepted, belong in the list.

The data represented by the list is based almost wholly upon specimens in the herbarium of the writer, and the name of the collector of each specimen cited is given in parenthesis except where the collection is that of the writer, in which case it is omitted.

IV. ACKNOWLEDGMENTS

The completeness of the survey of the rust flora of California here presented is in a large measure due to the assistance of the collectors whose names have been cited, who have furnished specimens or have given additional data regarding them. Especial obligations are due Mr. Ellsworth Bethel for a large amount of information regarding the heteroecious species, and for extended collections of grass and sedge inhabiting species from the southern part of the state both of which are poorly represented in most of the collections which have been made up to the present time. I desire also to express my thanks to Professor J. C. Arthur, who read over the entire list of species here presented and made many valuable suggestions. It will also be obvious that much help has been derived from such portions of Arthur's arrangement of the North American species of Uredinales (*North American Flora*, vol. 7) as have been published, of the critical work of Holway in that portion of his *North American Uredineae* which has been published, and Jackson's *Uredinales of Oregon*, published in the *Memoirs of the Brooklyn Botanic Garden*.

V. GENERAL FEATURES OF THE UREDINALES

The Uredinales represent a group of fungi whose vegetative parts consist of a much branched and septate mycelium, which develops in the leaves, branches, and fruits of certain seed producing plants and ferns and abstracts nourishment from the cells of the surrounding tissues by means of haustoria. The reproductive parts are represented by five different types of spores, one or more of which are frequently lacking and which differ greatly as to form and size as well in the mode of production and germination. The different spore forms are the following:

Spermatia, designated by the symbol O, are produced in subglobose or flask-shaped spermogonia and are minute hyaline bodies, which can be made to germinate but do not appear to perform any important function in the life history. They usually appear with or slightly before the aecia.

Aeciospores, designated by the symbol I, are produced in cup-shaped or cylindrical aecia, which have a more or less well developed peridium, or in masses, frequently surrounded by paraphyses, in which a peridium is lacking. They are always one-celled and are formed by the successive abstriction of the ends of closely packed

hyphae. They have a hyaline epispore and a number of germ pores but rapidly lose their ability to germinate.

Urediniospores designated by the symbol II, are usually produced in subepidermal sori and ultimately burst through the epidermis as light brown or yellow pulverulent masses. They are produced singly at the ends of hyphae, are always one-celled, either globose, elliptical or pyriform, possess several germ pores and are either echinulate or tuberculate.

Teliospores, designated by the symbol III, are formed like the urediniospores, but sometimes appear singly, either in or on the tissues of the host. They usually possess a definite pedicel and may be fascicled or compacted into a crust or a cylindrical column. Each spore may consist of a single cell or of as many as twenty cells; each cell usually possesses a single germ pore. They possess a thick epispore, which is dark brown or black in color. On germination they produce a thick promycelial tube, which ultimately produces four cells, each of which develops a single basidia and sporidium. When the sporidia germinate they produce short tubes which are able to penetrate the tissues of the proper host plant. The formation of basidia is one of the most distinguishing characteristics of the group.

Many species show well characterized alternation of generations on host plants belonging to the same species (autoecious) or on host plants belonging to different species (heteroecious).

VI. LIST OF SPECIES

The genera are arranged alphabetically, and the species numbered consecutively throughout the paper.

AECIDIUM

Under this form genus are grouped those aecial forms which have a true peridium and for which no other stage has as yet been recognized.

1. **Aecidium Collinsiae** Ell. and Ev.
   Bull. Washb. Lab., vol. 1, p. 4, 1884.

On *Collinsia bicolor* Benth., Berkeley and Ukiah.

2. **Aecidium Graebnerianum** Hennings
   Hedwigia, vol. 37, p. 273, 1898.

On *Habenaria dilatata* (Pursh.) Hook., Death Valley (Coville); on *H. leucostachys* Wats., Mount Eddy (Copeland).

3. **Aecidium Triglochinis** Diet. and Holw.

Erythea, vol. 7, p. 98, 1899.

On *Triglochin concinna* Davy, Lassen County, type collection (Davy).

4. **Aecidium Valerianellae** (Biv.) Bernh.

Stirp. Rar. Sci., vol. 4, p. 28.

On *Valerianella congesta* Lindr., Mill Valley and Applegate.

BAEODROMUS ARTH.

Ann. Mycologici, vol. 3, p. 19, 1905.

Cycle of development includes pycnia and telia only. Telia subepidermal but erumpent; teliospores one-celled, ellipsoid, produced in chains but compacted into masses.

5. **Baeodromus californicus** Arthur. III

Ann. Mycologici, vol. 3, p. 19, 1905.

On *Senecio Douglasii* DC., Lytle Creek, San Bernardino Mountains (Parish).

BUBAKIA ARTH.

Résult. Sci. Cong. Bot. Vienne, p. 338, 1906.

Uredinia erumpent and pulverulent; urediniospores borne singly on pedicels. Telia subepidermal and indehiscent; teliospores one-celled, compacted into dense masses.

6. **Bubakia Crotonis** (Cke.) De Toni. II, III

Grevillea, vol. 6, p. 137, 1878.

On *Croton californicus* Müll. Arg., San Francisco, Long Beach (Bethel).

CALYPTOSPORA KÜHN

Hedwigia, vol. 8, p. 81, 1869.

Aecia erumpent, cylindrical with thin-walled peridium. Telia forming compact layers, indehiscent. Teliospores ellipsoid, usually four-celled.

7. **Calyptospora columnaris** (Alb. and Schw.) Kühn. 0, I, III

The aecial stage has been shown by Winter (Hedwigia, vol. 26, p. 28, 1887) to develop on a large number of species of *Abies*, including *A. magnifica* Murray and *A. concolor* Lindl. Arthur (Mycologia,

vol. 2, p. 231, 1910) also obtained aecia on potted plants of *A. Fraseri* (Pursh.) Lindl., which he had infected with *C. columnaris* from Nova Scotia, and Professor Frazier found aecia identical with those obtained by Arthur on *Abies balsamea* at Picto, Nova Scotia. In California Meinicke has collected similar aecia on *Abies concolor* Lindl. at Lake Tahoe, and on *A. magnifica* Murray at Heckel's, Lassen County.

Telia on *Vaccinium ovatum* Pursh. and *V. parvifolium* Smith, Santa Cruz, Marin, Mendocino and Humboldt counties; on *V. membranaceum* Pursh., Tahoe National Forest (Meinicke); on *V. Chandleri* Jepson, Mount Eddy (Copeland).

COLEOSPORIUM LEV.

Ann. sci. nat. I, Bot., vol. 8, p. 373, 1847.

Aecia definite, erumpent; peridium colorless. Uredinia erumpent, pulverulent, spores in chains. Telia waxy, indefinite, liberated by disintegration of host only. Heteroecious.

8. **Coleosporium Bletiae** Diet. II, III

Hedwigia, vol. 37, p. 218, 1898.

On *Phajus Wallichii* Lindl. Reported by Arthur (*N. A. Flora*, vol. 7, p. 86) on plants imported from Japan, but not found by the writer although frequent inquiries were made for it.

9. **Coleosporium Campanulae** (Pers.) Lév. 0, I, II, III

Syn. Fung., p. 217, 1801; Ann. Sci. Nat., sér. 3, Bot., vol. 8, p. 373, 1847.

The aecial stage not known from California, but found on the Atlantic Coast on *Pinus rigida* and *P. virginiana*.

Uredinia and telia on *Campanula persicifolia* Linn., San Francisco. Probably a recent introduction as it was first noted by the writer in 1915 on the Exposition grounds.

10. **Coleosporium Madiae**, Cooke. II, III

Grevillea, vol. 7, p. 102, 1879; Sydow, Ann. Mycologici, vol. 2, p. 30, 1904.

Aecial stage probably represented by *Peridermium californicum* Arth. and Kern (see no. 35).

Uredinia and telia on *Madia capitata* Nutt., *M. anomala* Greene, *M. dissitiflora* (Nutt.) T. and G., *M. elegans* Don., *M. sativa* Molina, *M. Nuttallii* Gray, *Centromadia pungens* (H. and A.) Greene, and *Zonanthis corymbosa* (DC) Greene. Very common throughout the central portion of the state.

11. **Coleosporium Solidaginis** (Schw.) Thüm. 0, I, II, III

Bull. Torr. Club, vol. 6, p. 216, 1878.

The aecial stage probably represented by *Peridermium montanum* Arth. and Kern, which is reported from California by Hedgecock (Phytopathology, vol. 6, p. 64, 1916).

Uredinia common in the bay region on *Aster radulinus* Gray, *A. Menziesii* Lindl., *A. chilensis* Nee., and *Solidago californica* Nutt. On *Aster* sp., Yosemite Valley (Bethel); on *Solidago confinis* Gray, Pasadena (McClatchie).

CRONARTIUM FRIES

Observ. Myc., vol. 1, p. 220, 1815.

Aecia erumpent, inflated, usually forming galls. Uredinial spores born singly on pedicels. Telia erumpent, scattered; teliospores formed in chains which adhere to form a cylindrical column, one-celled, usually fusiform. Heteroecious.

12. **Cronartium coleosporioides** (Diet. and Holw.) Arthur. 0, I, II, III

Erythea, vol. 1, p. 247; N. A. Flora, vol. 7, p. 123, 1907.

The aecial stage (*Peridermium Harknessii* Moore) produces spheroid galls on *Pinus contorta* Dougl., *P. Sabiniana* Dougl. and *P. ponderosa* Dougl. Widely distributed throughout the Sierras, also at Mount Diablo (Blasdale and Bethel).

Uredinia and telia on *Castilleja foliolosa* H. and A., Berkeley (type of *Uredo coleosporioides* Diet. and Holw.), also Mill Valley (Bethel); on *C. latifolia* H. and A., and *C. Wightii* Elmer, Moss Beach (Mrs. Brandegee); on *C. miniata* Dougl., Lassen National Forest (Meinicke); on *C.* sp., Lake Tahoe (Bethel); on *C. Douglasii* Benth., San Mateo County (Copeland), on *C. Martini* Abrams, San Diego (Bethel).

13. **Cronartium filamentosum** (Peck) Hedgcock. 0, I, II, III

Bot. Gaz., vol. 7, p. 56, 1882; Phytopathology, vol. 2, p. 176, 1912.

The aecial stage produces slight hyperthrophy of branches on *Pinus ponderosa* Dougl. (*Peridermium filamentosum* Peck), Lake Tahoe; on *P. contorta* Dougl., Lake Tahoe, Plumas County (Meinicke).

Telia on *Castilleja miniata* Dougl., and according to Hedgcock not distinguishable morphologically from those of *Cronartium coleosporioides*, Lake Tahoe.

14. **Cronartium pyriforme** (Peck) Hedg. and Long. 0, I, II, III
Bull. Torr. Club, vol. 6, p. 13, 1875, and vol. 11, p. 50, 1884.

Aecia on *Pinus ponderosa* Dougl. (*Peridermium pyriforme* Peck) Rocky Gulch, Siskiyou County (Meinicke).

Uredinia and telia on *Comandra umbellata* (L) Nutt. (*Cronartium Comandrae* Peck), Shasta Springs. The genetic connection between these forms was shown by Hedgcock and Long (Bull. 247, U. S. Dept. Agr., 1914), also by Kirkwood (Phytopathology, vol. 5, p. 233, 1915).

15. **Cronartium Quercus** (Brond.) Schröt. 0, I, II, III
Sacc. Michelia, vol. 2, p. 308, 1881.

The aecial stage (*Peridermium Harknessii* Moore) produces globose galls often of large size on branches of *Pinus radiata* Don, and is sometimes very destructive. Also on *P. attenuata* Lemmon, *P. muricata* Don and *P. ponderosa* Dougl. in the central Coast Ranges.

Uredinia and more rarely telia on *Quercus agrifolia* Nee., *Q. Kellogii* Newb. and *Pasania densiflora* Oerst., Gilroy, Mount Diablo, Monterey (Meinicke), Mill Valley (Bethel), Santa Barbara (Bethel); on *Q. dumosa* Nutt., Pasadena (McClatchie).

There seems to be no essential difference between the eastern and western forms of this species, although culture experiments are needed to prove this conclusively. Meinicke (Phytopathology, vol. 6, p. 225, 1916) has shown that aecial spores from *Pinus radiata* could be made to reproduce aecia on the same host without an intervening stage; also that the fungus winters over in the uredinial stage on the leaves of *Quercus agrifolia.*

ERIOSPORANGIUM (BERTERO) LEV.

Ann. Sci. Nat., sér. 3, vol. 5, p. 269, 1846.

Aecia usually indefinite, peridium usually fragile. Uredinia definite, without paraphyses. Teliospores two-celled, usually pale or colorless.

16. **Eriosporangium evadens** (Hark.) Arthur. 0, I, II, III
Bull. Calif. Acad. Sci., no. 1, p. 34, 1884; Arthur, Résult. Sci. Cong. Bot. Vienne, p. 343, 1906.

The aecial stage is probably *Coleosporium Baccharidis* Cooke (Grevillea, vol. 9, p. 7, 1880), which produces galls often of large size on the branches of *Baccharis consanguinea* Greene and *B. pilularis* DC, similar to those of the bark-inhabiting species of *Peridermium.*

Uredinia and telia occur on the leaves of the same hosts, but as the sori are small they are easily overlooked. The genetic connection between the two forms has not been proven; but the frequency with which they are associated makes it probable that they are so related. It is common throughout the bay region and in southern California.

17. **Eriosporangium punctato-striatum** (Dietel and Neger) Arthur

Bot. Jahrb., vol. 22, p. 357, 1896; N. A. Flora, vol. 7, p. 213, 1912.

Aecia on stems and leaves on *Baccharis viminea* DC, but does not produce conspicuous galls.

Uredinia and telia on the same host (type of *Puccinia Baccharidis* Diet. and Holway), Santa Rosa, Los Gatos, Pasadena (McClatchie), San Bernardino (Parish), Paso Robles (Bethel), San Ysidro (Bartholomew), Lakeside (Bethel).

GYMNOSPORANGIUM HEDW.

Flora française, vol. 2, p. 216, 1805.

Aecia usually cylindrical but rarely cupulate; peridia membranous, the cells imbricate. Uredinia with one exception lacking. Telia naked, gelatinous, and somewhat elastic when mature; teliospores two-celled, sometimes three- to five-celled, by transverse septa, pedicels hyaline, usually long.

18. **Gymnosporangium Blasdaleanum** (Diet. and Holw.) Kern I, III

Erythea, vol. 3, p. 77, 1895; Kern, Bull. N. Y. Bot. Gard., vol. 7, p. 437, 1911.

Aecia on *Amelanchier alnifolia* Nutt. and *Crategus rivularis* Nutt., Sisson and Shasta Springs, type collection; on *Amelanchier alnifolia* Nutt., Hoopa Valley, Plumas County (Meinicke), Yosemite Valley and Lake Tahoe (Bethel), on *Amelanchier pallida* Greene and *Crategus Douglasii* Lindl., northern California (Kern.). This has the well developed peridium of a typical aecidium.

Telia on *Libocedrus decurrens* Torr. Sisson, Hoopa Valley, Siskiyou County (Copeland), Potter Valley (Purpus), Yosemite Valley and Lake Tahoe (Bethel); "widely distributed throughout the northern part of the state" (Meinicke). It sometimes produces witches' brooms of some size, but the spore masses, which appear as brown cushions on the smaller twigs and leaves, are not conspicuous.

The genetic connection between the two stages was first established by Arthur (Mycologia, vol. 1, p. 252, 1909, vol. 4, p. 57, 1912), who succeeded in growing aecia on *Crategus Pringlii* Sarg. from telia obtained from Corvallis, Oregon. From the latter state it is reported to be a rather serious pest by O'Gara (Science, vol. 39, p. 60, 1914), and by Jackson (Phytopathology, vol. 4, pp. 41, 261), attacking especially pears, quinces, and certain varieties of apples.

19. **Gymnosporangium Harknessianum** (Ell. and Ev.) Kern. I, III

Bull. N. Y. Bot. Gard., vol. 7, p. 441, 1911.

Aecia on *Amelanchier alnifolia* Nutt., Klamath River (Harkness), Plumas County (Meinicke).

What is believed to be the telial stage of this species has been collected by Meinicke on *Juniperus occidentalis* Hook., near Clio, Plumas County.

20. **Gymnosporangium koreaense** (P. Hennings) Jackson. I, III

Jour. Agr. Res., vol. 5, p. 1006, 1916.

Aecia on leaves of an ornamental species of *Pyrus* from a nursery near Oakland (D. P. T. MacDonald), but not otherwise reported from the state.

Telia not reported from California, but found in Oregon on *Juniperus chinensis Lindl.* (Jackson).

HYALOPSORA MAGN.

Ber. deut. bot. Ges., vol. 19, p. 582, 1901.

Aecia without peridium not conspicuous, irregularly dehiscent; aeciospores borne singly on pedicels, colorless. Uredinia with globoid peridium. Telia scattered, indehiscent; teliospores globoid, usually four-celled, colorless, wall thin and smooth.

21. **Hyalopsora Cheilanthis** (Peck) Arthur. II

Bull. Torr. Club, vol. 10, p. 62, 1883; Arthur, N. A. Flora, vol. 7, p. 113, 1907.

On *Pellaea andromedafolia* Kaulf., San Gabriel Cañon (Leroy Abrams); on *Ceratopteris triangularis* (Kaulf.) Underwood, Pasadena, type of *Uredo pasadenae* Sydow (McClatchie), Mount Tamalpais; Julian, San Diego County (Bethel).

22. **Hyalopsora laeviscula** (Diet. and Holw.) Arthur. II, III

Erythea, vol. 2, p. 127, 1894; Arthur, N. A. Flora, vol. 7, p. 113, 1907.

On *Polypodium californicum* Kaulf., Mount Tamalpais, type collections.

23. **Hyalopsora Polypodii** (DC) Magnus. I, II, III

Fl. franc., vol. 6, p. 81, 1815; Magnus, Ber. deut. bot. Ges., vol. 19, p. 582, 1901.

On *Filix fragilis* (L) Underwood, Humboldt County, King's River Cañon (Holway).

KUEHNEOLA MAGN.

Bot. Centralbl., vol. 74, p. 169, 1898.

Uredinia definite, erumpent, usually with paraphyses; urediniospores borne singly on pedicels, usually pale or colorless; telia erumpent, without paraphyses; teliospores three- to seven-celled, with transverse septa.

24. **Kuehneola uredinis** (Link) Arthur. 0, II, III

Willd. Sp. Plant, vol. 6, p. 123, 1824; Arthur, N. A. Flora, vol. 7, p. 186, 1912.

On *Rubus vitifolius* Cham. and Schlecht., reported by Arthur from California but not seen by the writer.

KUNKELIA ARTHUR

Bot. Gaz., vol. 63, p. 504, 1917.

This genus is based upon the fact, first shown by Kunkel (Bull. Torr. Bot. Club, vol. 40, p. 361, 1913, Am. Jour. Bot., vol. 1, p. 37, 1914), that the entire life cycle consists of a caeomoid stage associated with pycnia, the spores of which germinate like teliospores. It is not distinguishable morphologically from the aecial stage of the genus *Gymnoconia*, but the aecial spores of the genus last named germinate like true aecia spores, and there is an alternate stage not distinguishable from the telia of the genus *Puccinia*.

25. **Kunkelia nitens** (Schwein) Arthur. 0, I

Bot. Gaz., vol. 63, p. 504, 1917.

On *Rubus vitifolius* Cham. and Schl., Santa Rosa, on cultivated blackberry, Orange, Berkeley, Chico (Copeland), Glendora (Baker), Long Beach (Bethel). This is the widely distributed "orange rust" of the blackberry formerly known as *Caeoma nitens*.

26. **Kunkelia Rosae-gymnocarpae** (Dietel) Arthur

Hedwigia, vol. 44, p. 334, 1905; Arthur, Bot. Gaz., vol. 42, p. 505, 1917.

On *Rosa gymnocarpa* Nutt., Amador County, type collection (Hansen), Plumas County (Meinicke), Paso Robles and Yosemite Valley (Bethel). Very little is known about the life history of this rust, but its similarity to the preceding species makes it probable that it is also a short-cycle form. It appears very early in the spring and produces hypertrophy and ultimate death of the affected shoots.

MELAMPSORA CAST.

Observ., vol. 2, p. 18, 1843.

Aecia erumpent, peridia and pycnia wanting. Aeciospores globose with colorless walls. Uredinia erumpent, pulverulent, borne singly on pedicels. Telia in waxy layers, indehiscent; teliospores one-celled, prismatic or ellipsoid.

27. **Melampsora albertensis** Arthur. 0, I, II, III

Bull. Torr. Club, vol. 33, p. 517, 1906.

Aecia not reported from California but found in British Columbia and Colorado on *Pseudotsuga mucronata* (Raf.) Sudw. (*Caeoma occidentalis* Arthur).

Uredinia and telia on *Populus tremuloides* Michx., Dunsmuir (E. L. Smith); on *P. trichocarpa* T. and G., Yosemite Valley (Bethel). The genetic connection between these forms was established by Arthur (Mycologia, vol. 4, pp. 29, 58, 1912).

28. **Melampsora Bigelowii** Thüm. 0, I, II, III

Mitth. Forsty. Vers. Oest., vol. 2, p. 37, 1879.

The aecial stage (*Caeoma Bigelowii* Thum. Arth.) not reported from California but found elsewhere on *Larix Lyalii* Parl.

Uredinia and telia on *Salix lasiandra* Benth. and *S. lasiolepis* Benth., Berkeley; on *S. laevigata* Bebb and *S. exigua* Nutt., Long Beach (Bethel). Extremely common and widely distributed.

29. **Melampsora Lini** (Pers.) Desmaz. 0, I, II, III

Syn. Fungi, p. 216, 1901; Desmaz, Pl. Crypt., fasc. 41, no. 2049, 1850.

On *Linum micranthum* Gray, Sisson; on *L. digynum* Gray, Amador County (Hansen). Also reported by Arthur (N. A. Flora, vol. 7, p. 102); on *L. congestum* Gray, *L. Lewisii* Pursh.; *L. Breweri* Gray, and *L. drymarioides* Curran. This species was shown to be autoecious by Arthur (Jour. of Mycol., vol. 13, p. 207, 1907).

30. **Melampsora occidentalis** Jackson. II, III

Phytopathology, vol. 7, p. 354, 1917.

On *Populus trichocarpa* T. and G., Siskiyou, Trinity, and Shasta counties (Meinicke); on *P. Fremontii* Wats., San Bernardino (Parish). These specimens were formerly referred to *Melampsora Medusae* Thüm., from which the species named above differs in a number of minor characters. Still another specimen collected by Bethel on *Populus alba* L. at San José, which has also been referred to *M. Medusae*, has not been satisfactorily named.

MELAMPSOROPSIS (SCHROET) ARTHUR

Résult. Sci. Cong. Bot. Vienne, p. 338, 1908.

Aecia erumpent but laterally flattened; peridium firm. Aeciospores ellipsoid to globoid, walls colorless. Uredinia erumpent, pulverulent. Telia waxy; teliospores in chains, one-celled, oblong or cuboid, walls colorless.

31. **Melampsoropsis Piperiana** Arthur. II

N. A. Flora, vol. 7, p. 120, 1907.

On *Rhododendron californicum* Hook, Humboldt County.

32. **Melampsoropsis Pyrolae** (DC) Arthur. 0, I, II, III

Fl. franc., vol. 6, p. 99, 1815; Arthur, Résult. Sci. Cong. Bot. Vienne, p. 338, 1906.

The aecial stage not reported from California but collected by Hedgcock on *Picea Engelmanii* Parry. The genetic connection of this species with *Peridermium conorum Piceae* was shown by Fraser (Mycologia, vol. 4, p. 183, 1912).

On *Pyrola uliginosa* Torr., Sisson (Holway).

NEORAVENELIA LONG

Bot. Gaz., vol. 35, p. 131, 1903.

Aecia erumpent, without peridium; aeciospores in chains, wall colored. Uredinia erumpent; urediniospores borne singly on pedicels, wall colored. Telia erumpent; teliospores like those of *Ravenelia*.

33. **Neoravenelia Holwayi** (Dietel) Long. 0, I, II, III

Hedwigia, vol. 33, p. 61, 1894; Bot. Gaz., vol. 35, p. 131, 1903.

On *Prosopis juliflora* (Sw.) DC, San Bernardino County (McClatchie).

NYSSOPSORA ARTH.

Résult. Sci. Cong. Bot. Vienne, p. 342, 1906.

Telia erumpent; teliospores three-celled by oblique partitions, laterally flattened; walls deeply colored, spinous.

34. **Nyssopsora echinata** (Lev.) Arth. III
Ann. Sci. Nat., sér. 3, Bot., vol. 9, p. 247, 1848; Arthur, *op. cit.*

On *Oenanthe californica* Wats., San Francisco, Santa Cruz (Thomson); on *Selinum pacificum* Wats., Santa Rosa and Hoopa Valley.

PERIDERMIUM

Under this form genus are grouped those aecial forms for which no other stages are known and which resemble the aecia of *Coleosporium* and *Cronartium*.

35. **Peridermium californicum** Arth. and Kern
Mucologia, vol. 6, p. 118, 1914.

On *Pinus radiata* Don., Monterey (Bethel). This is believed to be the aecial stage of *Coleosporium Madiae* by Meinicke, but the data upon which this conclusion is based has not yet been published.

36. **Peridermium Ephedrae** Cooke
Indian Forester, vol. 3, p. 95, 1877; Arthur and Kern, Bull. Torr. Club, vol. 33, p. 420, 1906.

On *Ephedra californica* Wats., San Diego (Bethel), Riverside County (Parish). Conspicuous on account of its large, orange colored spore masses; see Standley (Plant World, vol. 13, p. 61, 1909).

PHRAGMIDIUM LINK.

Ges. nat. Freunde, Berlin, vol. 7, p. 30, 1915.

Aecia erumpent, usually indefinite and surrounded by paraphyses. Aeciospores in chains, globoid, with colorless walls. Uredinia erumpent, usually with paraphyses; urediniospores borne singly on pedicles. Telia erumpent, usually definite and without paraphyses; teliospores two-celled or more by transverse septa with two or more lateral pores.

37. **Phragmidium Andersoni** Shear. I, II, III
Bull. Torr. Club, vol. 29, p. 453, 1902.

On *Potentilla fruticosa* L., Mount Eddy, Siskiyou County (Copeland).

38. **Phragmidium disciflorum** (Tode) James. 0, I, II, III
Fungi Meckl., vol. 1, p. 16, 1790; James. Contr. U. S. Nat. Herb., vol. 3, p. 276, 1895.

On cultivated roses of the hybrid perpetual class, common throughout the state.

39. **Phragmidium imitans** Arthur. I, II, III
N. A. Flora, vol. 7, p. 165, 1912.

On *Rubus leucodermis* Dougl., Sisson, Shasta Springs, Yosemite Valley and Rionido; on cultivated varieties of raspberry rather frequent and sometimes destructive.

40. **Phragmidium Ivesiae** Sydow. I, II, III
Ann. Mycologici, vol. 1, p. 329, 1903.

On *Potentilla Blaschkeana* Turcz., Sisson, Lake Tahoe, Lassen County (Davy); on *P. glandulosa* Lindl., Modoc County (Meinicke); on *P. Hallii* Rydb., Lake Tahoe (Holway); on *P. Elmeri* Rydb., Donner Lake (Heller).

41. **Phragmidium montivagum** Arth. 0, I, II, III
Torreya, vol. 9, p. 24, 1909.

On *Rosa gymnocarpa* Nutt., Pine Ridge, Fresno County (Hall and Chandler).

42. **Phragmidium occidentale** Arthur. 0, I, II, III
Greene, Plantae Bakerianae, vol. 2, p. 3, 1901.

On *Rubus parviflorus* Nutt., Shasta Springs, Los Gatos, Berkeley, Mount Tamalpais, Rionido, Yosemite Valley, and Lake Tahoe.

43. **Phragmidium Rosae-californicae** Diet. I, II, III
Hedwigia, vol. 44, pp. 125, 333, 1904.

On *Rosa californica* Cham. and Schl., *R. gymnocarpa* Nutt., *R. sonomensis* Greene, and *R. minutifolia* Englm. Of frequent occurrence throughout the Coast Ranges. The aecia produce hypertrophy of the young shoots early in the season; later they appear on the mature leaves, which they injure but little.

PILEOLARIA CAST.

Obs., vol. 1, p. 22, 1842.

Uredinia erumpent, with paraphyses; urediniospores borne singly on pedicels, walls colored. Telia erumpent, definite; teliospores borne on pedicels, one-celled, flattened laterally, wall deeply colored, very verrucose.

44. **Pileolaria Toxicodendri** (Berk. and Rav.) Arthur. 0, II, III
Grevillea, vol. 3, p. 56, 1874; Arthur, N. A. Flora, vol. 7, p. 147, 1907.

On *Rhus diversiloba* T. and G., common in the Coast Ranges, Catalina Island (Bartholomew).

POLYTHELIS ARTHUR

Résult. Sci. Cong. Bot. Vienne, p. 341, 1906.

Telia erumpent, definite, without peridium. Teliospores forming heads attached by fragile pedicels to a common stalk, which is inconspicuous; two-celled by a transverse septum, easily separating at the septum.

45. **Polythelis Thalictri** (Chev.) Arthur. 0, III
Chev., Fl. Paris., vol. 1, p. 417, 1826; Arthur, Résult. Sci. Cong. Bot. Vienne, p. 341, 1906.

On *Thalictrum Fendleri* Engìm., Lake Tahoe.

PUCCINIA PERS.

Sp. Pl., vol. 6, p. 67, 1825.

Aecia erumpent, cupulate, or cylindrical; aeciospores in chains, globoid or ellipsoid, wall colorless. Uredinia erumpent definite, without peridium; urediniospores borne on pedicels, wall colored, echinulate or verrucose. Telia erumpent, sometimes long covered by the epidermis; teliospores two-celled; wall colored, with a single pore to each cell.

Telia on Graminaceae

46. **Puccinia abundans** (Pk.) Jackson. I, III
Mem. Brooklyn Bot. Gard., vol. 1, p. 229, 1918.

The aecial stage of this species (*Aecidium abundans* Pk.) is occasionally found on *Symphoricarpos racemosus* Michx., Berkeley, Santa Rosa.

Telia not definitely reported from California but to be expected on species of *Festuca*.

47. **Puccinia adspersa** Diet. and Holw. II, III
Erythea, vol. 3, p. 81, 1895.

On unknown grass, Modoc County (F. P. Nutting). This species seems to differ but little if at all from *Puccinia Clematidis* (DC) Lagerh.

48. **Puccinia anomala** Rostr. I, II, III

Thüm, Myc. Univ., no. 831.

Aecia, not reported from California, but in Russia on species of *Ornithogalum* (Mycol. Cent., vol. 4, p. 70, 1914).

Uredinia and telia on *Hordeum vulgare* L., Davis (L. R. Jones).

49. **Puccinia Aristidae** Tracy. II, III

Jour. of Mycol., vol. 9, p. 281, 1893.

On *Aristida bromoides,* Waterman's Hot Springs, San Bernardino County (Parish).

50. **Puccinia Hordei** Fuckel. II, III

Jahrb. Ver. Nat. Nassau, vol. 15, p. 16, 1860.

Uredinia and telia on *Hordeum murinum* L., Berkeley, San Diego, and Long Beach (Bethel); on *H. Gussonianum* Parl., Los Angeles (Bethel).

51. **Puccinia Clematidis** DC, Lagerh. I, II, III

Troniso Mus. Parsh., vol. 17, p. 47, 1895.

Aecia on *Clematis lasiantha* Nutt. and *C. ligusticifolia* Nutt. (*Aecidium Clematidis* DC), Berkeley, Atlas, Napa County, and Sisson, Mount Wilson (Bethel); on *Aquilegia truncata* F. and M. (*Aecidium Aquilegiae* Pers.), Berkeley, Acorn, Humboldt County; on *Clematis pauciflora* Nutt., San Diego County (LeRoy Abrams); on *Thalictrum Fendleri,* Lake Tahoe.

Uredinia and telia on *Bromus villosus* Forst., Berkeley, Ukiah, Ontario, San Bernardino, Long Beach (Bethel); on *B. hordaceus* L., San Diego (Bethel); on *B. carinatus* H. and A., Catalina Island (Bethel); on *B. marginatus* Nee., Willits (Hitchcock); on *Elymus triticoides* Buckl. Catalina Island (Bethel); on *E. condensatus* Presl. (Bethel); on *E. glaucus* Buckl., Campbell (H. B. Humphrey), and near Mount Shasta (E. Palmer).

52. **Puccinia Cynodontis** Desm. II, III

Exsiccati, vol. 3, no. 655.

Uredinia on *Cynodon dactylon* Pers., Sacramento, Anaheim; "very common throughout southern California" (Bethel). Telia produced only during the winter season.

53. **Puccinia Epicampis** Arthur. II, III

Bull. Torr. Bot. Club, vol. 33, p. 662, 1901.

On *Epicampes ringens* Benth., San Diego (Bethel).

54. **Puccinia Fendleri** (Tracy and Earle) Jackson. I, III

Mem. Brooklyn Bot. Gard., vol. 1, p. 246, 1918.

Aecia (*Aecidium Fendleri* Tracy and Earle) on *Berberis pinnata* Lag., Berkeley. Collected but once and but poorly developed. This was formerly taken to be the aecial stage of *Uropyxis sanguinea* (Erythea, vol. 3, p. 131, 1895) and its specific identity is still an open question.

Telia not reported from California but to be expected on species of *Koeleria.*

55. **Puccinia glumarum** (Schmidt) Erikss. and Henn. II, III

Zeitschr. f. Pflanzenkr., vol. 4, p. 1917, 1894.

On *Hordeum murinum* L., near Tehachipi (A. G. Johnson). This is one of the most destructive grain rusts in Europe but apparently it is not common in California. See Humphrey and Johnson, Phytopath., vol. 6, p. 80, 1916.

56. **Puccinia graminella** (Spez.) Diet. and Holw. I, III

Erythea, vol. 3, p. 80, 1895.

On *Stipa eminens* Cav., Berkeley. This is the only rust which produces its aecia on a grass; the aecia are easily overlooked.

57. **Puccinia Holcina** Erikss. II, III

Ann. Sci. Nat., sér. 8, vol. 9, p. 274, 1899.

Uredinia on *Notholcus lanatus* (L) Nash, extremely common in the bay region, Humboldt County, southern California (Bethel).

58. **Puccinia interveniens** (Pk.) Bethel comb. nov. 0, I, III

Pk. Bull. Torr. Bot. Club, vol. 29, p. 74, 1883.

Aecia (*Aecidium roestilioides* Ell. and Ev.) on *Sidalcea malvaeflora* (Moc. and Sesse) Gray, Oakland Hills, Mount Tamalpais, San Francisco, Pasadena (McClatchie), San Diego, Monterey, and Julian (Bethel); on *S. asprella* Greene, Butte County (Heller); on *Malvastrum Thurberi* Gray, San Diego and San Jacinto (Bethel); on *M. ambigua,* Victorville and Granite Mountain, near Julian (Bethel).

Telia (*Puccinia Burnettii* Griff.) on *Stipa pulchra* Hitch., Santa Cruz (Griffiths); on *S. speciosa*, Victorville and Granite Mountain (Bethel); on *S.* sp., Mill Valley and San Diego (Bethel); on *Oryzopsis hymenoides* Ricker, Victorville (Bethel).

The connection between these forms has been established by Bethel by repeated cultures with both telia and aecia, the first being made in Colorado in 1912. His numerous collections of both aecia and telia in 1916 and 1918 in southern California, not far from the type locality of *Roestelia interveniens* establish the validity of the combination given above. The aecia have very short peridia, split almost to the base, as in the form genus *Roestilia;* the telia form sori from one to three inches in length, especially on the sheaths, which are tardy in rupturing.

59. **Puccinia luxuriosa** Sydow. II, III

Monogr. Ured., vol. 1, p. 812, 1904.

On *Sporobolus airoides* Torr., Lakeside, Riverside County (Bethel).

60. **Puccinia Majanthae** (Schrum.) Arth. and Holw. 0, I, II, III

Bull. Lab. Nat. Hist. Iowa, vol. 5, p. 188, 1901.

Aecia not reported from California but elsewhere on species of *Polygonatum* and *Convallaria.*

Uredinia and telia on *Phalaris minor* Retx., Long Beach (Bethel) and Palo Alto (Thomson); on *P. californica* H. and A., Montara Point, San Mateo County (Copeland).

61. **Puccinia montanensis** Ellis. I, II, III

Jour. of Mycol., vol. 7, p. 274, 1883.

Aecia on *Hydrophyllum capitatum* Dougl. and *H. occidentale* Gray (*Aecidium Hydrophyllae* Peck.), Humboldt and Mendocino counties, Amador County (Hansen); on *Phacelia californica* Cham. and *P. nemoralis* Greene (*Aecidium Phaceliae* Peck), Berkeley; on *Phacelia tanacetifolia* Benth., Carmel.

Telia on *Hordeum nodosum* L., Catalina Island (Bethel).

62. **Puccinia Poarum** Niels. II, III

Bot. Tids., vol. 2, p. 26, 1877.

Uredinia on *Poa annua* L., and *P. pratensis* L., Berkeley, Long Beach (Bethel).

Telia not reported from California.

63. **Puccinia poculiformis** (Jacq.) Wettst.
Verhl. Zool. Ges. Vienne, vol. 35, p. 544, 1885.

Aecia on species of Berberis, but not reported from California.

Uredinia and telia on *Avena fatua* L., *A. barbata* Brot., and *A. sativa* L.; on *Hordeum murinum* L., *H. Gussonianum* Parl. and *H. sativum* Jessen; on *Phleum pratense* L.; on *Agrostis alba* L. and *A. diegoensis* Vas.; on *Elymus condensatus* Presl.; on *Lamarckia aurea* Moench; on *Dactylis glomerata* L.; on *Panicularia pauciflora* (Presl.) Kze. Frequent throughout the state. This is the "black stem rust" found especially on the culms of oats, and in some seasons decidedly destructive. It includes several well defined biological forms, which are discussed by Stakeman and Piemeisel (Phytopathology, vol. 6, p. 99, 1918).

64. **Puccinia procera** Diet. and Holw. II, III
Erythea, vol. 1, p. 249, 1893.

On *Elymus condensatus* Presl., Pasadena (McClatchie), Berkeley, Long Beach, and San Diego (Bethel).

65. **Puccinia purpurea** Cke. II, III
Grevillea, vol. 5, p. 15, 1879.

On *Andropogon sorghum* var. *halepensis* L., Gilroy, Santa Ana (Bethel).

66. **Puccinia Rhamni** (Pers.) Wettst. I, II, III
Ver. zool.-bot. Ges. Wien, p. 544, 1885.

Aecia not reported from California, but to be looked for on species of *Rhamnus*.

Uredinia and telia on *Polypogon monspeliensis* Desf., Berkeley, Humboldt County, Ontario, Santa Barbara; on *Avena barbata* Brot., San Diego (Bethel); on *Lamarckia aurea* Moench, Los Angeles (Bethel) on *Lolium perenne* L., and *L. multiflorum* Lam., Long Beach (Bethel).

67. **Puccinia sejuncta** Sydow. 0, I, II, III
Ann. Mycologici, vol. 1, p. 326, 1903.

Aecia on *Hieracium* sp., Sisson (Holway).

68. **Puccinia Sorghi** Schw. II, III
Trans. Am. Philos. Soc., ser. 2, vol. 4, p. 295, 1832.

On *Zea mays* L., frequent but not destructive.

69. **Puccinia Stipae** (Opiz.) Arth. 0, I, II, III
Bull. Iowa Agri. Coll., p. 160, 1884.

Aecia not definitely reported from California, but this stage is known to occur on nine different chicoriaceous and carduaceous genera (Bethel, Phytopathology, vol. 6, p. 99, 1916).

Uredinia and telia on *Stipa setigera* Presl., Berkeley; on *S. pulchra* Hitch., San Diego, Coronado Island, and Long Beach (Bethel); on *S. eminens Andersoni* Vassey, San Diego (Bethel); on *Oryzopsis hymenoides* Ricker, Victorville (Bethel).

70. **Puccinia subnitens** Dietel. I, III
Erythea, vol. 3, p. 81, 1895.

Aecia on *Spergularia Clevelandii* (Greene) Robinson, Long Beach; on *S. macrotheca* (Hornem) Heynh; on *Tholypodium laciniatum* Endl. and *Heliotropium curassavicum* L., Lassen County (Davy); on *Abronia pinetorum* Jepson, San Jacinto (Bethel); on *Isomeris arborea* Nutt., San Diego (Jones). Shown by Bethel (Phytopathology, vol. 7, p. 92, 1917) to develop on eighty-five different species of host plants, representing fifty-two genera and nineteen families.

Telia on *Distichlis spicata* Greene, Redwood City, "common from Los Angeles to San Diego," San Jacinto (Bethel).

71. **Puccinia Triticina** Erikss. II, III
Ann. Sci. Nat., sér. 8, Bot., vol. 9, p. 270, 1899.

Frequent on certain varieties of wheat, Berkeley, San Francisco, Anaheim, Long Beach (Bethel). It is closely related to *P. Clematidis*.

Telia on Cyperaceae

72. **Puccinia Asterum** (Schw.) Kern. I, II, III
Mycologia, vol. 9, p. 224, 1917.

Aecia on *Aster* sp., Lake Tahoe and Calaveras Co., Seabright (Mrs. Clemens); on *A. occidentalis*, Yosemite Valley (Bethel).

Telia on *Carex* sp., Lake Tahoe, Seabright (Mrs. Clemons).

73. **Puccinia atro-fusca** (Dudley and Thomson) Holway. II, III
Jour. of Mycol., vol. 10, pp. 55, 228, 1904.

On *Carex Douglasii* Bott. and *C. usta* Bailey, San Bernardino County (Dudley and Thompson). This species is peculiar in that it produces large numbers of amphispores, and hence was first placed in the genus *Uromyces*.

74. **Puccinia canaliculata** (Schw.) Lagerh. 0, I, II, III

Tromso Mus. Aarsh., vol. 17, p. 51, 1894.

Aecia on *Xanthium Canadense* Mill, Lakeside (Bethel).

Telia on *Cyperus esculentus* L., Long Beach and San Bernardino (Bethel).

75. **Puccinia Caricis** (Schum.) Rebent. 0, I, II, III

Fl. neomarch, p. 356, 1804.

Aecia on *Urtica gracilis holosericea* Jepson, Berkeley.

Uredinia and telia on *Carex obnupta* Bailey, Berkeley.

76. **Puccinia Eleocharidis** Arthur. III

Prelim. List Iowa Ured., p. 158, 1884.

On *Eleocharis montana* (H. B. K.) R. and S., Long Beach (Bethel).

77. **Puccinia Grossulariae** (Schum.) Lager. 0, I, II, III

Aecia on *Ribes divaricatum* Dougl., Berkeley, San Francisco, Sisson.

Telia not reported in California but probably present on species of *Carex*.

78. **Puccinia McClatchieana** Diet. and Holw. II, III

Erythea, vol. 2, p. 127, 1895.

On *Scirpus microcarpus* Presl., San Francisco, Pasadena (McClatchie).

79. **Puccinia obtecta** Peck. II, III

Bull. Buffalo Soc. Nat. Hist., vol. 1, p. 66, 1873.

On *Scirpus lacustris occidentalis* Wats., Sacramento; on *S. californicus* (Meyer) Britton and *S. Olneyi* Gray, Long Beach (Bethel); on *S. americanus* Pers., Escondido (Bartholemew).

80. **Puccinia patruelis** Arthur. I, II, III

Mycologia, vol. 1, p. 245, 1909.

Telia not reported in California, but probably present on species of *Agoseris* and *Crepis*.

Uredinia and telia on *Carex marcida* Boott., San Bernardino (Bethel and Parish).

81. **Puccinia Peckii** (De Toni) Kell. I, III
Jour. of Mycol., vol. 8, p. 20, 1902.

Aecia on *Onagra Hookeri* (T. and G.) Small, Yosemite Valley, Giant Forest, King's River Cañon (Holway), San Bernardino (Bethel).

Uredinia and telia on *Carex siccata* Dewey, Yosemite Valley (Bethel).

Telia on Liliaceae

82. **Puccinia Alliorum** (DC) Corda. I, II, III
Fl. franc., vol. 6, p. 82, 1815; Corda Icones, vol. 4, p. 12, 1840.

On *Allium serratum* Wats. type of *Puccinia Blasdalei* Diet. and Holw., Antioch and Mount Diablo; on *A. falcifolium* H. and A., Benicia (Bigelow).

Unlike the European *P. Alliorum* I and III are produced on the same plants.

83. **Puccinia Asparagi** DC. 0, I, II, III
Fl. franc., vol. 2, p. 595, 1805.

On *Asparagus officinalis* L. Common throughout the state, and the source of large losses to growers. The life history and methods of combating it have been exhaustively studied by Professor R. E. Smith, Calif. Agr. Exp. Sta., Bulls. 165, 172.

84. **Puccinia Calochorti** Peck. I, III
Bot. Gaz., vol. 6, p. 228, 1881.

On *Calochortus albus* Dougl., Hoopa Valley; on *C. venustus* Benth., *C. Maweanus* Leichtl., Plumas County (Horne); on *C. bisceptrum* Wats., King's River Cañon, type of *Puccinia Holwayi* Diet. (Holway); on *C. elegans* Pursh., type of *Puccinia anachorita* Ell. and Hark. (Harkness).

85. **Puccinia granulispora** Ell. and Gall. I, II, III
Bull. Torr. Club, vol. 22, p. 61, 1895.

On *Allium precox* Brandegee, San Bernardino (Parish).

86. **Puccinia mesomegala** Berk. and Cooke. III
25th Ann. Rept. N. Y. State Mus., p. 111, 1873.

On *Clintonia uniflora* (Menzies) Knuth, Amador County (Hansen), and Siskiyou County (Meinicke).

87. **Puccinia Moreniana** Dudley and Thomson. III
Jour. of Mycol., vol. 10, p. 53, 1904.

On *Brodiaea capitata* Benth., Searsville Lake, San Mateo County (Dudley and Thompson).

88. **Puccinia nodosa** Ell. and Hark. II, III
Bull. Calif. Acad. Sci., vol. 1, p. 27, 1884.

On *Brodiaea capitata* Benth., Berkeley, Ukiah.

89. **Puccinia Veratri** Duby. I, II, III
Bot. Gall., vol. 2, p. 890, 1830.

Aecia not definitely reported from California, but known to develop on species of *Epilobium*.

Uredinia and telia on *Veratrum californicum* Durand, Placer County, Lake Tahoe, Yosemite Valley (Bethel), Modoc County (F. P. Nutting).

Telia on Iridaceae

90. **Puccinia Iridis** (DC) Wallr. II, III
Encyc., vol. 8, p. 224, 1808; Rabh. Krypt. Flora, vol. 1, p. 23, 1844.

Uredinia on *Iris longipetala* Herb., *I. Douglasiana* Herb., *I. missouriensis* Nutt., common in the Coast Ranges. Occasionally found on certain cultivated varieties of *I. germanica*, *I. xiphium* L., *I. alata* Poir., and *I. pumila*. Telia very rare.

Telia on Santalaceae

91. **Puccinia Comandrae** Peck. III
Bull. Torr. Club, vol. 11, p. 49, 1884.

On *Comandra umbellata* (L) Nutt., Shasta Springs, Fresno County (Holway).

Telia on Aristolochiaceae

92. **Puccinia Asarina** Kze. III
Kunze and Schmidt, Mykol., vol. 1, p. 70, 1817.

On *Asarum Lemmoni* Wats., Sisson, King's River Cañon (Holway); on *A. caudatum* Lindl., Olema.

93. **Puccinia Cynanchi** Lagerh. III
Biol. Soc. Brot., p. 129, 1889.

On *Funastrum hirtellum* (Gray) Schltr., Palm Springs (Parish).

Telia on Polygonaceae

94. **Puccinia Acetosae** (Schum.) Koern. II, III

Hedw., vol. 15, p. 184, 1876.

On *Rumex occidentale* Wats., and *R. acetosella* L., Berkeley; on *R. persicarioides* L., Long Beach (Bethel).

95. **Puccinia amphispilusa** Diet. and Holw. II, III

Erythea, vol. 3, p. 79, 1895.

On *Polygonum Davisiae* Brewer, Lake Tahoe; on *P. Newberryi*, Lassen County, type collection (F. P. Nutting).

96. **Puccinia Bistortae** (Str.) DC. II, III

Fl. franc., vol. 6, p. 61, 1815.

On *Polygonum bistortoides* (Pursh.) Small, Sherwood, Mendocino County, King's River Cañon (Holway).

97. **Puccinia Polygoni-amphibii** Pers. 0, I, II, III

Syn. Method. Fung., p. 227, 1801.

Aecia not reported from California but found in Europe on species of Geranium. Uredinia and telia on *Polygonum Muhlenbergii* Wats., San Francisco, Los Gatos, Victorville (Bethel); on *P. lapathifolium* L., San Bernardino (Parish); on *P. acre* H. B. K., Berkeley, San Mateo County (Baker); on *P. amphibium* L., Palo Alto (Scherfee); on *P. hydropiperoides* Michx., Los Angeles County (LeRoy Abrams).

98. **Puccinia punctiformis** Diet. and Holw. II, III

Erythea, vol. 2, p. 128, 1894.

On *Rumex salicifolius* Weinn., Berkeley, type collection; on *R. hymenosepalus* Torr., Berkeley, in cultivation.

Telia on Chenopodiaceae

99. **Puccinia Dondiae** Arthur. II, III

Bull. Torr. Bot. Club, vol. 42, p. 592, 1915.

On *Dondia intermedia* (Wats.) Heller, San Diego (Marcus E. Jones).

Telia on Cruciferae

100. **Puccinia Holboellii** (Hornem) Rostr. III
Fl. Danica, vol. 37, p. 11, 1840; Rostr. Fungi Groen., p. 34, 1886.

On *Arabis Holboelli* Hornem, Yosemite Valley, Pasadena, type of *Puccinia palefaciens* Diet. and Holw. (McClatchie), San Diego County (Bethel); on *A. Breweri* Wats., Mount Diablo (Bioletti); on *A. arcuta* Gray, King's River Cañon (Holway); on *A. perennans* Wats., San Bernardino (Parish).

Telia on Ranunculaceae

101. **Puccinia Delphinii** Diet. and Holw. III
Hedwigia, vol. 32, p. 29, 1893.

On *Delphinium* sp., King's River Cañon (Holway).

102. **Puccinia gemella** Diet. and Holw. III
Sydow, Monogr. Ured., vol. 1, p. 541, 1903.

On *Caltha Howellii* Greene, reported from California by Holway (N. A. Ured., vol. 1, p. 6).

Telia on Saxifragaceae

103. **Puccinia Heucherae** (Schw.) Diet. III
Ber. deut. bot. Ges., vol. 9, p. 42, 1892.

On *Heuchera micrantha* Dougl. (*Puccinia congregata* Hark.), frequent in the Coast Ranges; on *Tellima grandiflora* (Pursh.) Dougl., Shasta Springs; on *Tellima affinis*, Mount Tamalpais (R. S. Gray).

Telia on Crassulaceae

104. **Puccinia Rhodiolae** B. and Br. III
Ann. Mag. Nat. Hist., ser. 2, vol. 5, p. 452, 1850.

On *Sedum* sp., King's River Cañon (Holway).

Telia on Rhamnaceae

105. **Puccinia Mesnieriana** Thüm. III
Mycotheca Universalis, vol. 9, p. 834, 1877.

On *Rhamnus crocea* Nutt., Ukiah, Napa County, Pasadena (McClatchie); Fresno County (Holway), San Diego (Parish), Santa Barbara, and Yosemite Valley (Bethel), Mount Tamalpais (Harkness), type of *Puccinia digitata* Ell. and Hark.; on *R. ilicifolius* Kellogg, Mount Diablo; on *R. insularis* Kellogg, Claremont (Baker).

Telia on Malvaceae

106. **Puccinia lobata** B. and C. III
Grevillea, vol. 3, p. 54, 1874.

On *Sida hederacea* (Dougl.) Torr., Holtville, Imperial County, Long Beach (Bethel).

107. **Puccinia Malvacearum** Bertero. III
Gay, Hist. de Chille, vol. 8, p. 43, 1852.

On *Malva borealis* Wallm., *M. parviflora* L. and *Althea rosea* Cav., common throughout the state; on *Sida hederacea* (Dougl.) Torr., Suisun (Davy). At the Botanic Garden of the University of California has been found on *Malva moschata* Linn., *M. sylvestris* L., *M. crispa* L., *M. oxyloba* Boiss., *Lavatera maritima* Gouan, *L. arborea* L., *L. sylvestris* Brot., *L. plevica* Sims, and *L. assurgentifolia* Kell.

108. **Puccinia Sherardiana** Koern. III
Hedwigia, vol. 16, p. 19, 1877.

On *Malvastrum Thurberi* Gray, Fresno County (Holway), San Diego, and San Jacinto (Bethel); on *M. splendidum* Kellogg, Claremont (Baker); on *Sidalcea spicata* Greene, Lake Tahoe (Bethel).

109. **Puccinia Sphaeralceae** Ell. and Ev. I, III
Am. Naturalist, p. 428, 1879.

On *Sidalcea* sp., Humboldt County.

Telia on Violaceae

110. **Puccinia effusa** Diet. and Holw. 0, I, III
Erythea, vol. 3, p. 81, 1895.

On *Viola lobata* Benth., Dunsmuir (Holway).

111. **Puccinia Violae** (Schum.) DC. 0, I, II, III
Pl. Saell., vol. 3, p. 224, 1803; Fl. franc., vol. 6, p. 62, 1915.

On *Viola nephrophylla* Greene and *V. adunca longipes* Sisson; on *V. glabella* Nutt., Sherwood; on *V. ocellata* T. and G., Ukiah.

Telia on Onagraceae

112. **Puccinia Circaeae** Pers. III
Tent. Disp. Meth. Fung., p. 39, 1797.

On *Circaea pacifica* Aschers and Magnus, Sisson and Weitchpec, Trinity County.

113. **Puccinia Epilobii-tetragoni** (DC) Wint. 0, I, II, III
Rabh. Krypt. Flora, vol. 1, p. 214, 1884.

On *Epilobium franciscanum* Barbey, San Francisco, and Olema; on *E. paniculatum* Nutt., Rionido and Los Gatos, Pasadena (McClatchie), San Mateo County (Thomson); on *E.* sp., King's River Cañon, type of *Puccinia intermedia* Diet. and Holw.

114. **Puccinia Gayophyti** Billings. I, II, III
Bot. Gaz., vol. 7, p. 56, 1882.

On *Gayophytum diffusum* T. and G., Sisson, Calaveras Big Trees (Dudley); on *G. pumilum* Wats., Mount Eddy (Heller); on *G. ramossissimum* T. and G. (Harkness).

115. **Puccinia heterantha** Ell. and Ev. 0, I, II, III
Erythea, vol. 1, p. 204, 1893.

On *Taraxia ovata* (Nutt.) Small, Berkeley and Atlas, Napa County; on *T. graciliflora* (H. and A.) Small (A. Kellogg and W. G. W. Harford). The aecia appear very early in the spring and cause hypertrophy and ultimate destruction of the first leaves. The uredinia and telia appear later and are less destructive. The genetic relation between the two stages was shown by the writer (Rep. Calif. Exp. Sta., p. 227, 1894).

116. **Puccinia Ludwigiae** (Ell. and Ev.) Holw. 0, I, III
Proc. Phil. Acad. Sci., p. 153, 1893; Holway, N. A. Ured., vol. 1, p. 72, 1907.

On *Ludwigia natans* Ellis, San Bernardino (Parish).

117. **Puccinia Oenotherae** Vize. II, III
Grevillea, vol. 5, p. 109, 1877.

On *Clarkia elegans* Dougl., *C. concinna* (F. and M.) Greene, and *C. rhomboidea* Dougl., type of *Puccinia Clarkiae* Peck. On *Godetia rubicunda* Lindl., *G. amoena* Don., *G. biloba* (Durand) Wats., *G. grandiflora* Lindl. On *Boisduvalia densiflora* (Lindl.) Wats. and *B. sparsiflora* Heller, type of *Puccinia Boisduvaliae* Peck. On *Eulobus californicus* Nutt., type of *Puccinia Eulobi* Diet. and Holw. On *Oenothera strigulosa* T. and G. and *O. gauraeflora* T. and G. On *Sphaerostigma spirale* (Lehm) Walp., *S. hirtella* (Greene) Small, *S. viridescens* (Lehm) Walp., *S. micrantha* (Hornem) Walp., and *S. Veitchianum* (Hook) Small. Widely distributed and of frequent occurrence.

118. **Puccinia Zauschneriae** Sydow. I, II, III
Monogr. Ured., vol. 1, p. 436, 1906.

On *Zauschneria californica* Presl., common in the bay region and Coast Ranges. The aecial stage produces witches' brooms which soon wither away.

Uredinia and telia appear much later and are scarcely distinguishable from those of *Puccinia Oncotherae*. This species together with the forms included under numbers 113, 114, and 115 are considered forms of *P. Oenotherae* by G. R. Bisby (Am. Jour. Bot., vol. 3, p. 527, 1916).

Telia on Umbelliferae

119. **Puccinia asperior** Ell. and Ev. I, III
Bull. Washb. Lab., vol. 1, p. 3, 1884.

On *Leptotaenia dissecta* Nutt., Ukiah.

120. **Puccinia Cicutae** Lasch. II, III
Klotzsch Herb. Mycol., no. 787, 1845.

On *Cicuta Bolanderi* Wats., Suisun, Pajaro (Thompson); on *C. virosa* var. *californica* C. and R., San Francisco; on *C. occidentalis* Dougl., Sisson.

121. **Puccinia Cymopteri** Diet. and Holw. I, III
Bot. Goz., vol. 18, p. 255, 1893.

On *Cymopterus terebinthium* (Hook) T. and G., King's River Cañon (Holway).

122. **Puccinia Ellisi** De-Toni. II, III
Saccardo, Syllogi Fungorum, vol. 7, p. 651, 1888.

On *Angelica tomentosa* Wats., type of *Puccinia Bakeriana* Arthur, Palo Alto (Baker).

123. **Puccinia Hydrocotyle** (Link) Cke. II, III
Spec. Plant., vol. 6, p. 22, 1825; Grevillea, vol. 9, p. 14, 1880.

On *Hydrocotyle prolifera* Kell., San Mateo County (Thompson), San Bernardino (Parish), Pacific Grove (Mrs. Clemens).

124. **Puccinia Jonesii** Peck. I, III
Bot. Gaz., vol. 6, p. 226, 1881.

On *Peucedanum dasycarpum* T. and G., Mount Diablo, Palo Alto (Thompson), on *P. Hassei* C. and R., Atlas, Napa County.

125. **Puccinia Lindrothii** Sydow. I, III
Acta Soc. Fauna et Flora Fennica, vol. 22, p. 62, 1902.

On *Drudeophytum Hartwegii* (Gray) C. and R., Berkeley; on *Velaea arguta* (F. and G.) C. and R., Mount Lowe (Bethel).

126. **Puccinia Osmorrhizae** (Peck) Cke. and Peck. 0, I, II, III
Rep. N. Y. State Mus., vol. 24, p. 92, 1872; vol. 29, p. 73, 1878.

On *Osmorrhiza nuda* Torr. and *O. occidentalis* (Nutt.) Torr., common in the Coast Ranges, Calaveras County (Dudley), King's River Cañon (Holway); on *O. brevipes*, Sonoma County (Heller).

Telia on Primulaceae

127. **Puccinia melanconioides** Ell. and Hark. I, II, III
Bull. Calif. Acad. Sci., no. 1, p. 27, 1884.

On *Dodecatheon Hendersonii* Gray, common throughout the state; on *D. Jeffreyi* Van Houtte, San Bernardino Mountains (Parish).

Telia on Gentianaceae

128. **Puccinia Gentianae** (Str.) Link. II, III
Spec. Plant, vol. 2, p. 73, 1824.

On *Gentiana oregana* Englm., Mount Tamalpais; on *G. Menziesii* Griseb., Mendocino County (Davy).

Telia on Convolvulaceae

129. **Puccinia Convolvuli** (Pers.) Cast. I, II, III
Cat. Pl. Marseilles, p. 202, 1845.

On *Convolvulus luteolus* Gray and *C. subacaulis* Gray, common throughout the bay region; on *C. occidentalis* Gray, Pasadena (McClatchie).

130. **Puccinia Cressae** (DC) Lagh. I, II, III
Biol. Soc. Brot., p. 131, 1889.

On *Cressa cretica* L., Napa County, Calaveras County, Lassen County (Davy), Catalina Island (McClatchie), Mountain View (Thompson), southern California (Bethel).

131. **Puccinia Dichondrae** Mont. I, III
Gay, Fl. Chil., vol. 8, p. 46, 1853; also Syll. Crypt., p. 313, 1856.

On *Dichondra repens*, Forst., San Diego and Orange County (M. E. Jones).

Telia on Polemoniaceae

132. **Puccinia Giliae** Hark. II, III

Bull. Calif. Acad. Sci., no. 1, p. 34, 1884.

On *Linanthus ciliatus* (Benth.) Greene, Mount Diablo (Harkness); on *Collomia grandiflora* Dougl., Sisson; on *Gilia gilioides* (Benth.) Greene, Tuolumne County; on *G. capitata* Dougl., Klamath River, Humboldt County (H. P. Chandler); on *Navarretia atractyloides* (Benth.), H. and A., Pasadena (McClatchie).

133. **Puccinia plumbaria** Peck. I, III

Bot. Gaz., vol. 6, p. 238, 1881.

On *Microsteris gracilis* (Dougl.) Greene, Mendocino County; on *Linanthus ciliatus* (Benth.) Greene, Calaveras County; on *Gilia californica* Benth., Snow Mountain, type of *Puccinia gilicola* Hennings (Purpus).

Telia on Boraginaceae

134. **Puccinia Cryptanthis** Diet. and Holw. II, III

Erythea, vol. 1, p. 249, 1893.

On *Cryptanthe Torreyana* (Gray) Greene, Fresno County (Holway); on *C. flaccida* (Lehm) Greene, Fresno County (Holway).

Telia on Labiateae

135. **Puccinia distorta** Holway. II, III

Ann. Mycol., vol. 3, p. 20, 1905.

On *Hyptis Emoryi* Torr., Palm Springs (Parish).

136. **Puccinia mellifera** Diet. and Holw. I, III

Erythea, vol. 1, p. 25, 1893.

On *Salvia mellifera* Benth., Pasadena (McClatchie), San Jacinto and Santa Barbara (Bethel); Carmel (Mrs. Clemens); on *Audibertia Palmeri* Gray, San Jacinto (Bethel).

137. **Puccinia Menthae** Pers. I, II, III

Synopsis Fung., p. 227, 1801.

On *Mentha canadensis* L., Suisun, San Bernardino (Parish), San Ysidero (Bartholomew); on *M. sativa* L., Pajaro (Thompson); on *Micromeria Chamissonis* (Benth.) Greene, common in the bay region, type of *Puccinia Micromeriae* Dudley and Thompson. On *Monardella*

villosa Benth., common in the Coast ranges, type of *Puccinia Monardellae* Dudley and Thompson; on *M. odoratissimum* Benth., Lake Tahoe; on *M. lanceolata* Gray, Grass Valley (C. J. Wright); on *M. viridis* Jepson, Napa County; on *M. micrantha* Gray, San Bernardino (Parish).

Telia on Solanaceae

138. **Puccinia Chamaesarachae** Sydow. I, III

Ell. and Ev., N. A. Fungi, no. 1476; Sydow, Monogr. Ured., vol. 1, p. 263, 1902.

On *Chamaesarache nana* Gray, Truckee (Bethel).

139. **Puccinia globosipes** Peck. II, III

Bull. Torr. Club, vol. 12, p. 34, 1885.

On *Lycium californicum* Nutt., San Pedro (McClatchie); on *L. Andersoni Wrightii* Gray, San Bernardino County (Parish).

Telia on Scrophulariaceae

140. **Puccinia Adenostegiae** Arthur. III

Bull. Torr. Club, vol. 29, p. 231, 1902.

On *Adenostegia pilosa* Greene, Palo Alto (LeRoy Abrams); on *A. rigida* Jepson, San Diego County (Mrs. Brandegee).

141. **Puccinia Antirrhini** Diet. and Holw. II, III

Hedwigia, vol. 36, p. 298, 1899.

On *Antirrhinum majus* L., common in the bay region and southern California; on *A. Nuttallianum* Benth., San Bernardino (Parish); on *A. virga* Gray, Ukiah (Heller) and Lake County (Jepson). The writer has also found it possible to infect with this species plants of the native *A. vagans* Gray, and the exotic *A. assurgens, A. nudicum, Linaria amethystina, L. delphinifolia, L. bipartita, L. melanthera,* and *L. marocanna.* The "snapdragon rust" has been a troublesome pest in California for many years, and is reported to have appeared in the neighborhood of Chicago, in Ohio, and Indiana (Phytopathology, vol. 4, p. 400, 1914). It was first found by the writer at San Leandro in 1896.

142. **Puccinia Castillejae** (Diet. and Holw.) Arthur, comb. nov. II, III

Erythea, vol. 1, p. 247, 1893.

Uredinia (*Uredo Castilleiae* Diet. and Holw.) amphigenous, scattered, round or oval, 0.5 mm. across, early naked, pulverulent, light

cinnamon brown, ruptured epidermis, not evident; urediniospores broadly ellipsoid or globoid, 16–24 by 20–29μ; wall golden brown, thick, 2–3μ, moderately to closely echinulate, the pores 3, equatorial.

Telia not seen; teliospores broadly ellipsoid to ovoid, 18–23 by 23–29μ, rounded above, slightly narrowed below, slightly or not constricted at the septum; wall chestnut to dark golden brown, 2–3μ thick, moderately thickened at the apex, 5 to 7μ, smooth; pedicel colorless, short, fragile.

On *Castelleja foliolosa* H. and A., Berkeley, Coahuila Valley (Bethel).

143. **Puccinia Cordylanthi** Blasdale, sp. nov. II, III

Sori containing both urediniospores and teliospores, scattered, minute, rarely confluent, erumpent; urediospores globose or ellipsoid, cinnamon brown, with two or three germ-spores; teliospores oblong, not clavate nor constricted at the septum, apex not thickened; 15–24μ by 29–41μ, brown, pedicel short and hyaline.

On stems and leaves of *Cordylanthes filifolia* Nutt., collected by E. Bethel at Cajon Pass, San Bernardino County.

This species is more closely related to *P. Adenostegiae* Arth. than to *P. Anthirrhini* Diet. and Holw.; it differs from the latter in the characters of the sori, and from both in the form and size of the teliospores. These differences are shown in the figures given below, which represent the results of the measurement of forty mature spores of each of the three species.

	Average measurement	Extreme measurement
Puccinia Antirrhini	21.9 by 51.37μ	16–26 by 41–64μ
Puccinia Adenostegiae	21.75 by 42.33μ	18–29 by 32–49μ
Puccinia Cordylanthi	20.68 by 35.13μ	15–24 by 29–41μ

144. **Puccinia Palmeri** Diet. and Holw. III

Erythea, vol. 7, p. 98, 1899.

On *Penstemon confertus* Dougl., Lake Tahoe; on *P. Newberryi* Gray, Alpine County (Hansen).

145. **Puccinia Pentastemonis** Peck. III

Bull. Torr. Club, vol. 12, p. 35, 1885.

On *Pentstemon Roezli* Regel., Cisco (L. S. Smith); on *P. deustus* Douglas, Sloate, Plumas County (Horne); on *P. azureus* Benth., Kewville (Heller); on *P. Bridgesii* Gray, King's River Cañon (Holway).

146. **Puccinia rufescens** Diet. and Holw. I, III
Bot. Gaz., vol. 18, p. 253, 1893.

On *Pedicularis semibarbatus* Gray, Lake Tahoe, King's River Cañon (Holway), Mount San Antonio (McClatchie).

147. **Puccinia Wulfeniae** Diet. and Holw. III
Erythea, vol. 3, p. 79, 1895.

On *Synthyris rotundifolia* Gray, Ukiah.

Telia on Rubiaceae

148. **Puccinia punctata** Link. 0, I, II, III
Obs. Myc., *in* Ges. naturf. Freunde, Berlin, vol. 2, p. 30, 1816.

On *Galium aparine* L., Berkeley; on *G. triflorum* Michx., Sisson and Shasta Springs, type of *Puccinia chondroderma* Lindr.

149. **Puccinia rubifaciens** Johans. III
Bot. Centralbl., vol. 28, p. 394, 1888.

On *Galium californicum* H. and A., King's River Cañon (Holway).

Telia on Caprifoliaceae

150. **Puccinia Symphoricarpi** Hark. III
Bull. Calif. Acad. Sci., vol. 1, p. 35, 1884.

On *Symphoricarpos racemosus* Michx., very common in the bay region and the Coast Ranges.

Telia on Compositae

151. **Puccinia Absinthi** DC. II, III
Fl. franc., vol. 6, p. 56, 1815.

On *Artemisia heterophylla* Nutt., Berkeley, Los Gatos, Napa and Rionido; on *A. tridentata* Nutt., Lassen County (Davy) and Cajon Pass (Bethel); on *A. Suksdorfii* Piper, Los Gatos (Heller); on *A. dracunculoides* Pursh., San Jacinto (Bethel); on *A. elatior* (T. and G.) Rydberg, Visalia (Holway); on *A. Douglasiana* Bess., Santa Barbara (A. D. E. Elmer). This species is frequently included under *P. Tanaceti* DC, from which it differs but little.

152. **Puccinia Asteris** Duby. III
Bot. Gall., vol. 2, p. 888, 1830.

On *Aster chilensis* Nee., Berkeley; on *A. yosemitanus* Greene, Yosemite Valley.

153. **Puccinia Balsamorrhizae** Peck. II, III

Bull. Torr. Club, vol. 11, 49, 1884.

On *Balsamorrhiza sagittata* Nutt., Lake Tahoe, Amador County (Hansen), Lassen County (F. P. Nutting); on *B. deltoidea* Nutt., King's River Cañon (Holway).

154. **Puccinia Chrysanthemi** Rose. II, III

Bull. Soc. Mycol., Franc., vol. 17, p. 92, 1900.

On *Chrysanthemum indicum* DC, frequent throughout the state and sometimes a serious pest. Telia found but once in southern California by Bethel. This species is now widely distributed over Europe and North America. It was first observed by the writer at Berkeley in 1910.

155. **Puccinia Cirsii** Lasch. II, III

Rabh. Fungi Europ, No. 89, 1859.

On *Cirsium edule* Nutt. and *C. lanceolatum* (L) Scop., Berkeley; on *C. undulatum* (Nutt.) Spring, Antioch; on *C. Breweri* (Gray) Jepson, King's River Cañon, type of *Puccinia californica* Dietel and Holw. (Holway); on *C. occidentale* (Nutt.), Jepson, San Francisco; on *C. Drummondii acaulescens* (Gr.) Cov., King's River Cañon (Holway); on *C. quercetorum* (Gray) Jepson, Santa Cruz (Thompson).

156. **Puccinia conferta** Diet. and Holw. III

Erythea, vol. 1, p. 250, 1893.

On *Artemisia heterophylla* Nutt., King's River Cañon, type collection (Holway), Ukiah (Holway and Blasdale); on *A. californica* Less., Pasadena, type of *Puccinia recondita* Dietel (McClatchie).

157. **Puccinia crepidicola** Sydow. II, III

Oestr. bot. Zeitschr., vol. 51, p. 17, 1901.

On *Crepis pleurocarpa* Greene, Mount Eddy, Siskiyou County (C. F. Baker).

158. **Puccinia Crepidis-acuminatae** Sydow. II, III

Oestr. bot. Zeitschr., vol. 51, p. 27, 1901.

On leaves and stems of *Crepis acuminata* Nutt., King's River Cañon (Holway); on *C. pleurocarpa*, Siskiyou and Trinity counties (G. D. Butler).

159. **Puccia Franseriae** Sydw. II, III

Ann. Mycol., vol. 1, p. 326, 1903.

On *Franseria dumosa* Gray, Palm Springs.

160. **Puccinia Grindeliae** Peck. III

Bot. Gaz., vol. 4, p. 127, 1879.

On *Grindelia* sp., Julian, San Diego County (Bethel).

161. **Puccinia Harknessii** Vize. II, III

Grevillea, vol. 7, p. 11, 1878.

On *Lygodesmia spinosa* Nutt., Lassen County (Davy); on *Ptiloria exigua* Nutt., San Bernardino County (Parish).

162. **Puccinia Helianthellae** (Peck) Arthur. II, III

Bull. Torr. Club, vol. 31, p. 4, 1904.

On *Helianthella nevadensis* Greene, Nevada County (Heller); on *H. californica* Gray, Nevada County (M. E. Jones).

163. **Puccinia Helianthi** Schw. II, III

Syn. Fung. Carol., p. 73, 1822.

On *Helianthus annuus* L., frequent throughout the state; on *H. lenticularis* Dougl., Fresno County (Holway) and Pasadena (McClatchie); on *H. debilis* Nutt, in cultivation, Berkeley.

164. **Puccinia Hemizoniae** Ell. and Tracy. II, III

Jour. of Mycol., vol. 7, p. 43, 1891.

On *Hemizonia luzulaefolia* DC, Berkeley and Santa Rosa; on *H. Clevelandii* Greene, Santa Rosa; on *H. citrina* Greene, Marin County (Heller); on *Lagophylla congesta* Greene, Berkeley, type of *Puccinia Lagophyllae* Diet. and Holw.

165. **Puccinia Hypochoeridis** Oud. II, III

Nederl. Kruidk. Archief., (2), vol. 1, p. 175, 1872.

On *Hypochaeris glabra* L., Berkeley, San Francisco, Mount Diablo, Monterey (Bethel).

166. **Puccinia intermixta** Peck. I, III

Bot. Gaz., vol. 4, p. 231, 1879.

On *Iva axillaris* Pursh., Lassen County (Davy).

167. **Puccinia investita** Schw. I, III

N. A. Fungi, no. 2932; Peck, Rep. N. Y. St. Mus., p. 117, 1872.

On *Gnaphalium chilense* Spreng. San Francisco; on *G.* sp., Mount Tamalpais (Bethel).

168. **Puccinia Millefolii** Fuckl. III

Symb. Myc., vol. 55, 1869.

On *Achillea millefolium* L., San Francisco (Bethel).

169. **Puccinia splendens** Vize. III

Grevillea, vol. 7, p. 11, 1878.

On *Hymenoclea salsola* T. and G., Mojave Desert (Parish); on *H. monogyra* T. and G. (Griffiths).

170. **Puccinia Stephanomeriae** Sydow. II, III

Monogr. Ured., vol. 1, p. 117, 1904.

On *Stephanomeria lactucina* Gray, Sisson; on *S. chicoriaceum* Gray, Pasadena (McClatchie), Mount Wilson (Bethel); on *S. runcinata*, Victorville (Bethel); on *Ptiloria carduacea*, Claremont (Baker).

171. **Puccinia Taraxaci** (Rebent) Plowr. II, III

Plowr. British Ured. and Ustilig., p. 186, 1889.

On *Taraxacum Taraxacum* (L), Karst., Berkeley and Sisson.

172. **Puccinia Troximontis** Peck. II, III

Bot. Gaz., vol. 6, p. 227, 1881.

On *Agoseris plebica* Greene, Santa Rosa, Berkeley and San Francisco; on *A. barbellata*, Mount Eddy (Copeland); on *A. hirsuta* (Hook) Greene, Berkeley.

173. **Puccinia variolans** Hark. III

Bull. Calif. Acad. Sci., no. 1, p. 15, 1884.

On *Aplopappus squarrosus* H. and A., Pasadena (McClatchie); on *Tetradymia glabrata* Gray, Lassen County (Davy).

174. **Puccinia Wyethiae** (Peck) Ell. and Ev. II, III

Bot. Gaz., vol. 7, p. 46, 1882; Ell. and Ev., N. A. Fungi, no. 2987.

On *Wyethia angustifolia* Nutt., Berkeley and Ukiah, also Los Angeles, Long Beach, and San Ysidro (Bethel).

175. **Puccinia Xanthii** Schw. III

Syn. Fung. Carol, p. 73, 1822.

On *Xanthium canadense* Mill., San Francisco, Suisun, Fresno County (Holway), Pasadena (McClatchie), San Bernardino (Parish), Los Angeles, and Long Beach (Bethel).

PUCCINIASTRUM OTTH.

Mitth. nat. Ges. Bern, p. 71, 1861.

Aecial stage similar to that of the genus Coleosporium, on the leaves of species of *Pinus* and *Abies*. Urediniospores borne singly on pedicels, walls colorless. Telia indehiscent in layers in or beneath the epidermis. Teliospores usually prismatic, two- to four-celled.

176. **Pucciniastrum Goodyerae** (Tranz.) Arthur. II

Arthur, N. A. Flora, vol. 7, p. 105, 1907.

On *Goodyera Menziesii* Lindl., Mount Eddy (Copeland).

177. **Pucciniastrum pustulatum** (Pers.) Dietel. 0, I, II, III

Dietel, *in* Engler and Prant., Natürl. Pflanzenfam., vol. 1, p. 47, 1897.

The aecial stage not definitely known from California, but shown by Frazier (Mycologia, vol. 4, p. 175, 1912) to develop on *Abies balsamea* (L) Mill.

Uredinia and telia on *Epilobium franciscanum* Barbey; on *E. adenocaulon* Treal., *E. coloratum* Muhl., *E. holosericeum* Treal., and *E. californicum* Haussek. Common in the Coast Ranges. Uredinia found throughout the year.

178. **Pucciniastrum Pyrolae** (Pers.) Dietel. II, III

Gmel. Syst. Nat., vol. 2, p. 1474; Dietel, *in* Engler and Prant., Natürl. Pflanzenfam., vol. 1, p. 47, 1897.

On *Pyrola picta* Smith and *P. secunda* L., Sisson and Mount Tallac, Plumas County (Horne); on *Chimaphila umbellata* (L) Nutt., Siskiyou County (Meinicke).

179. **Pucciniastrum sparsum** (Wint.) Ed. Fischer. II, III

Rabh. Krypt. Flora, vol. 1, p. 245, 1881; Beiträg. Krypt. Schweiz., vol. 2, p. 469, 1904.

On *Arbutus Menziesii* Pursh., Mount Tamalpais, type of *Uredo Arbuti* Diet. and Holw.; on *Arctostaphylos patula* Greene, Sisson, type of *Uredo Copelandi* Sydow; on *A. Hookeri* Don., Antonio Station, Santa Barbara County (Brandegee).

RAVENELIA Berk.

Gard. Chron., p. 132, 1853.

Uredinia erumpent, without peridium; urediniospores borne singly on pedicels, wall colored. Teliospores fascicled on compound stalks, one- or two-celled, forming heads bordered by hyaline cysts.

180. **Ravenelia arizonica** Ell. and Ev. II, III

Bull. Torr. Club, vol. 22, p. 363, 1895.

On *Prosopis juliflora* (Sw.) DC, San Diego (Bethel).

181. **Ravenelia versatilis** (Peck) Diet. II, III

Hedwigia, vol. 33, p. 368, 1894.

On *Acacia Greggii* Gray, San Bernardino (Toumey), Banning (Parish).

TRANZSCHELIA Arth.

Résult. Sci. Cong. Bot. Vienne, p. 340, 1906.

Aecia cylindrical; aeciospores globoid; wall colored. Uredinia erumpent; urediniospores borne singly on pedicels mixed with paraphyses. Telia erumpent, pulverulent; teliospores attached to a common stalk by short inconspicuous pedicels.

182. **Tranzschelia punctata** (Pers.) Arth. 0, I, II, III

Ann. Bot. Usteri, vol. 20, p. 135, 1796; Arthur, *op. cit.*

Aecia not known from California but found on various species of *Hepatica*, *Anemone* and *Thalictrum* (*Aecidium punctatum* Pers.) in the eastern United States.

Uredinia and more rarely telia on cultivated peach, plum, prune, almond, and apricot, especially in the southern part of the state, but widely distributed. This is the "prune rust" which is sometimes the source of considerable losses to fruit growers.

UREDINOPSIS Magn.

Atti Cong. Bot. Geneva, p. 167, 1893.

Aecia similar to those of *Coleosporium*, found on leaves of species of *Abies*. Uredinia larger and more conspicuous than the aecia, the agglutinated spores ejected from the delicate peridium in a long mucilaginous filament. Telia indehiscent; teliospores four-celled, with thin wall.

183. **Uredinopsis Copelandii** Sydow. I, II, III
Ann. Mycologici, vol. 2, p. 34, 1904.

Aecia not definitely reported from California, but elsewhere on species of *Abies*.

Uredinia and telia on *Athyrium cyclosorum* Rupr., Sisson (Copeland).

184. **Uredinopsis Pteridis** Diet. and Holw. I, II, III
Ber. d. deut. bot. Gesell., Bd. 13, p. 331, 1895.

Aecia (*Peridermium pseudo-balsameum* Arthur and Kern) on *Abies grandis* Lindl., Eureka. Reported by Hedgcock (Mycologia, vol. 4, p. 141, 1912) on *A. lasiocarpa* Nutt., and *A. nobilis* Lindl.

Uredinia and telia on *Pteris aquilinum pubescens* Underwood. Sisson, Lake Tahoe, San Francisco, Mount Tamalpais, Pasadena (McClatchie), Long Beach (Bethel). For culture experiments relating to this form see Weir and Hubert (Am. Jour. Bot., vol. 4, p. 328, 1917).

UREDO

Under this form genus are grouped the uredinial stages of certain species for which the mature stages are unknown.

185. **Uredo Acaenae** Ell. and Ev.
N. A. Fungi, no. 3150, 1894.

On *Acaena tridactyla* Presl., frequent in the bay region. Arthur (N. A. Flora, vol. 7, p. 174) takes this to be uredinia of *Phragmidium Ivesiae Sydow.*

186. **Uredo Gaillardiae** Diet. and Holw.
Erythea, vol. 7, p. 98, 1899.

On *Gaillardia aristata* Pursh, Dunsmuir (Holway).

187. **Uredo Nicotianae** Arthur, sp. nov.

Uredinia mostly hypophyllus, scattered upon discolored areas 1 to 1.5 cm. across, round, 0.2 to 0.5 mm. in diameter, early naked, applanate, subepidermal, pulverulent, pale cinnamon to whitish, ruptured epidermis evident; urediniospores globoid to broadly ellipsoid, 23 to 26μ by 24 to 32μ; wall colorless, 1.5 to 5μ thick, closely and coarsely verrucose, the pores obscure.* Collected in small amount at Rionido on *Nicotiana Bigelowii* Wats. The spores resemble those of a *Coleosporium*, although not in well defined chains.

* This description furnished by Professor J. C. Arthur.

188. **Uredo Phoradendri** Jackson

Mem. Brooklyn Bot. Gard., vol. 1, p. 285, 1918.

On *Phoradendron longispicum* Trelease, Chico (C. C. Thomas).

189. **Uredo Sphacelicola** Diet. and Holw.

Erythea, vol. 1, p. 248, 1893.

On *Sphacele calycina* Benth., Mount Tamalpais.

UROMYCES UNGER

Exanth. Pfl., p. 277, 1833.

Aecia erumpent, cupulate, or cylindrical; aeciospores in chains globoid or ellipsoid, often angular. Uredinia definite and without paraphyses; urediniospores borne singly on pedicels; wall colored, usually echinulate. Telia erumpent or long-covered by the epidermis; teliospores one-celled, wall firm, deeply colored, thick.

Telia on Graminaceae

190. **Uromyces Jacksonii** Arth. and Fromme. II, III

Torreya, vol. 15, p. 260, 1915.

On *Agrostis pallens* Trin., Atlas, Napa County; on *Hordeum nodosum* L, San Mateo County (Copeland).

191. **Uromyces Peckianus** Farlow. II, III

Proc. Am. Acad. Arts and Sci., p. 76, 1883.

Aecia on *Salicornia ambigua* Michx., *Chenopodium album* L., *C. murali* L., and *Atriplex* sp., Monterey (Bethel).

Uredinia and telia on *Distychlis spicata* Greene, Long Beach (Bethel), Ferndale (Davy and Blasdale). Probably common along the coast.

Telia on Cyperaceae

192. **Uromyces Scirpi** (Cast.) Burr. 0, I, II, III

Cat. Pl. Marseilles, p. 214, 1845; Bot. Gaz., vol. 9, p. 188, 1884.

Aecia on *Oenanthe californica* Wats., central California.

Uredinia and telia on *Scirpus pacificus* Britton, and *S. californicus* (Mey.) Britt, Long Beach (Bethel); on *S. paludosus* Nels., Escondido (Bartholomew).

Telia on Juncaceae

193. **Uromyces Junci** (Desmaz) Tul. 0, I, II, III
Ann. Sci. Nat., sér. 4, Bot., vol. 2, p. 148, 1854.

Aecia on *Ambrosia psilostachya* DC, San Jacinto and Coahuila Valley (Bethel).

Uredinia and telia on *Juncus balticus* Willd., Long Beach, Cajon Pass, and Victorville (Bethel), Mohave C. (Parish); Catalina Island (Bethel); on *J. leseurii* Boland, Sunol (Horne), Pasadena (McClatchie); on *J. textilis* Buch., Cajon Pass (Bethel), Pasadena (McClatchie), San Bernardino County (Parish); on *J. patens* Mey., San Mateo County (Copeland); on *J. Mexicanus* Willd., San Diego County (Chandler).

194. **Uromyces Junci-effusi** Sydow. II, III
Monogr. Ured., vol. 2, p. 290, 1910.

On *Juncus Xiphioides* E. Meyer, Ukiah and Mill Valley; on *J. phaeocephalus* Engelm., Long Beach (Bethel); on *J. nevadensis* Wats.

Telia on Liliaceae

195. **Uromyces aureus** Diet. and Holw. I, III
Hedwigia, vol. 32, p. 30, 1893.

On *Allium validum* Wats., King's River Cañon, type collection (Holway).

196. **Uromyces bicolor** Ellis. 0, I, II, III
Contr. U. S. Nat. Herb., vol. 4, p. 231, 1893; Bull. Torr. Club, vol. 24, p. 282, 1897.

On *Allium unifolium* Kell., Berkeley (type collection for *Uromyces aterrimus* Diet. and Holw.) and Sherwood, Mendocino County; on *A. validum* Wats., Sisson and Lake Tahoe.

197. **Uromyces Brodieae** Ell. and Hark. I, III
Bull. Calif. Acad. Sci., no. 1, p. 28, 1884.

On *Brodiaea capitata*, Berkeley, Mount Diablo, Yosemite Valley.

198. **Uromyces Chlorogali** Diet. and Holw. I, II, III
Erythea, vol. 1, p. 246, 1893.

On *Chlorogalum pomeridianum* (Ker.) Knuth, Berkeley, Mount Diablo, Atlas, Napa County, Palo Alto (Thompson).

199. **Uromyces Lilii** Clinton. 0, I, II, III
27th Rept. N. Y. State Mus., p. 103, 1875.

On *Lilium columbianum* Hansen, Sisson and King's River Cañon, type of *Uromyces Holwayi* Lagh. (Holway); on *L. rubescens* Wats., Shasta Springs; on *L. parvum* Kellogg, Lake Tahoe; on *L. Washingtonianum* Kell., Forest, Lassen County (F. P. Nutting).

200. **Uromyces Zygadeni** Peck. 0, I, II, III
Bot. Gaz., vol. 6, p. 239, 1881.

On *Zygadenus Fremonti* Torr., Pasadena (McClatchie), San Mateo County (Thompson). On *Z. sp.*, Santa Monica Mountains (Holway).

Telia on Polygonaceae

201. **Uromyces intricatus** Cooke. 0, I, II, III
Grevillea, vol. 7, p. 3, 1878.

On species of *Eriogonum* (*Uromyces Eriogoni* Ell. and Hark.) and *Chorizanthe* (*Uromyces Chorizanthis* Ell. and Hark), very common throughout the state. Arthur (N. A. Flora, vol. 7, p. 245) reports it from *Eriogonum cernum* Nutt., *E. dumosum* Greene, *E. elongatum* Benth., *E. fasciculatum* Benth., *E. latifolium* Smith, *E. nudum* Dougl., *E. parvifolium* Smith, *E. vimineum* Dougl., *E. virgatum* Benth., *Chorizanthe cuspidata* Wats., *C. robusta* Parry, and *C. pungens* Benth.

202. **Uromyces Polygoni** (Pers.) Fuckl. I, II, III
Symb. Mucol., p. 64, 1869.

Aecia very rare but collected by Bethel on *Polygonum aviculare* L. at Long Beach and San Jacinto.

Uredinia and telia very common throughout the state on the same host; on *P. erectum* L., Escondido (Bartholomew).

Telia on Chenopodiaceae

203. **Uromyces Betae** (Pers.) Lev. 0, I, II, III
Pers. Syn. Fung., p. 220, 1801; Ann. Sci. Nat., sér. 3, Bot., vol. 8, p. 375, 1847.

Aecia not reported from California but found in Europe and Australia.

Uredinia very common throughout the state on *Beta vulgaris* L. and *B. chicla*.

Telia found occasionally, specially upon seed-bearing plants.

204. **Uromyces Chenopodii** (Duby) Schroet. I, II, III
Duby., Bot. gall., vol. 2, p. 899, 1830; Schroeter, Kunze, Fung. Sel., no. 214, 1880.

Aecia, uredinia, and telia on leaves and stems of *Dondia multiflora* (Torr.) Heller, Long Beach, San Diego, and Point Firmin (Bethel); on *D. californica* (Wats.) Heller, Laguna Beach (H. W. Fawcett).

Telia on Portulaceae

205. **Uromyces Spragueae** Hark. I, III
Bull. Calif. Acad. Sci., vol. 1, p. 44, 1884.

On *Calyptridium umbellatum* Torr. Greene, Lake Tahoe, Yosemite Valley, Alpine County (Hansen), Plumas County (Meinicke), King's River Cañon (Holway).

Telia on Caryophyllaceae

206. **Uromyces Caryophyllina** (Schrank) Wint. 0, I, II, III
Sch. Baier. Fl., vol. 2, p. 666, 1789; Rab. Krypt. Flora, vol. 1, p. 149, 1881.

Uredinia and telia frequent throughout the state on certain varieties of *Dianthus caryophyllus* L., and sometimes the cause of large losses to florists. It was introduced into the eastern states about 1860 and first noted by the writer in California in 1896.

207. **Uromyces pulchellus** Ell. and Ev. II, III
Bull. Torr. Club, vol. 22, p. 57, 1895.

On *Silene Douglasii* Hook., Lake Tahoe.

Telia on Ranunculaceae

208. **Uromyces Aconiti-lycoctoni** (DC) Wint. I, II, III
Rabh. Krypt. Flora, vol. 1, p. 153, 1884.

On *Aconitum columbianum* Nutt., Sisson.

209. **Uromyces Jonesii** Peck. II, III
Bot. Gaz., vol. 7, p. 45, 1882.

On *Ranunculus flammula* L., King's River Cañon (Holway).

Telia on Leguminoseae

210. **Uromyces abbreviatus** Arthur. III
Bull. Torr. Club, vol. 42, p. 587, 1915.

On *Psoralea physoides* Dougl., Calistoga (Harkness), Pinehurst (Bethel).

211. **Uromyces albus** Diet. and Holw. I, III

Hedwigia, vol. 36, p. 297, 1897.

On *Vicia americana* Muhl., Crocker's Ranch, Mariposa County; on *V. americana truncata* Brewer, Sloate, Plumas County (Horne); on *V. californica* Greene, Cuyamaca Mountains (LeRoy Abrams), San Diego County (Bethel).

212. **Uromyces appendiculatus** (Pers.) Link. 0, I, II, III

Ann. Bot. Usteri, vol. 15, p. 16, 1795; Link, Observ., vol. 2, p. 26, 1816.

On *Phaseolus vulgaris* L. and *P. lunatus* L., frequent, especially in the southern part of the state, but not destructive.

213. **Uromyces Fabae** (Pers.) De Bary. 0, I, II, III

Neues Mag. Bot., vol. 1, p. 93, 1794; Ann. Sci. Nat., Bot., vol. 20, p. 80, 1863.

On *Lathyrus Bolanderi* Wats., *L. Jepsonii* Greene, *L. violaceus* Greene and *L. Torreyi* Gray, common in the bay region; on *L. sulfureus* Brewer, Plumas County (Horne).

214. **Uromyces fallens** (Desmaz) Kern

Plant Krypt., 1325; Kern, Phytopath., vol. 1, p. 6, 1911.

On *Trifolium pratense* L., of frequent occurrence in both the northern and southern portions of the state.

215. **Uromyces Glycyrrhizae** (Rabh.) Magn. II, III

Ber. deutsch. bot. Ges., vol. 8, p. 383, 1890.

On *Glycyrrhiza lepidota glutinosa* Wats., Tuolumne County, Walnut Grove, Cloverdale (Heller), Victorville (Bethel).

216. **Uromyces Lupini** B. and C. 0, I, II, III

Proc. Am. Acad. Arts and Sci., vol. 4, p. 127, 1858.

On *Lupinus formosus bridgesii* Green, *L. albifrons* Benth. and *L. Chamissonis* Esch., frequent in the bay region; on *L. rivularis* Dougl., San Bernardino County (Parish); on *L. Douglasii* Agardh, King's River Cañon (Holway); on *L. latifolius* Agardh., Santa Cruz County (Thompson).

217. **Uromyces Medicaginis** Pass. II, III

Thüm, Herb. Myc. Oecon., p. 155, 1874.

On *Medicago lupulina* L., Berkeley and Humboldt County; on *M. sativa* L., common, especially in the southern part of the state.

218. **Uromyces oblongus** Vize. I, III

Grevillea, vol. 5, p. 110, 1877.

On *Trifolium variegatum* Nutt., *T. gracilentum* T. and G., *T. microcephalum* Pursh., *T. microdon* H. and A., *T. dubium* Sibth., *T. roscidum* Greene, *T. ciliolatum* Benth., *T. depauperatum* Desv., *T. albopurpureum* T. and G., *T. Macraei* H. and A., *T. tridentatum* Lindl., *T. stenophyllum* Nutt., *T. oliganthum* Steud. Of frequent occurrence in the Coast Ranges and in the Sierras.

219. **Uromyces occidentalis** Diet. II, III

Hedwigia, vol. 42, p. 98, 1903.

On *Lupinus leptophyllus* Benth., Sisson; on *L. latifolius* Agardh, Boulder Creek and Berkeley.

220. **Uromyces punctatus** Schröt. 0, I, II, III

Abh. schles. Ges., vol. 48, p. 10, 1870.

Aecia on species of *Euphorbia* but not reported from America.

Uredinia and rarely telia on *Astragalus Menziesii* Gray, San Francisco; on *A. lentiginosus* Dougl., Kern County (Davy); on *A. leucopsis* Torr., Long Beach (Bethel); on *A. Preussii* Gray, Indio (E. A. Bessey); on *A. Purshii* Dougl., Hornbrook (Copeland); on *A. pycnostachys* Gray, San Mateo County (Baker); on *Lotus eriophorus* Greene, San Francisco (M. E. Jones); on *L. glaber* (Vogel) Greene, Long Beach (Bethel).

221. **Uromyces Trifolii** (Hedw.) Lev. I, II, III

An. Sci. Nat., sér. 3, Bot., vol. 8, p. 371, 1847.

On *Trifolium repens* L., frequent in both the northern and southern part of the state, but not destructive.

Telia on Euphorbiaceae

222. **Uromyces proeminens** (DC) Pass. 0, I, II, III

Fl. franc., vol. 2, p. 235, 1805; Rabh. Krypt. Flora Europ., p. 1795, 1873.

Aecia (*Aecidium Euphorbiae-hypericifoliae* Schw.) on *Euphorbia serpyllifolia* Pers., Berkeley, Olema, San Francisco, Amador County (Hansen), King's River Cañon (Holway), Catalina Island (McClatchie); on *E. polycarpa* Benth., Mojave County (Parish); on *E. albomarginata* T. and G., Inglewood (LeRoy Abrams).

Telia on Hypericaceae

223. **Uromyces Hyperici-frondosi** (Schw.) Arthur. 0, I, II, III
Schw. mat. Ges., Leipzig, vol. 1, p. 68, 1822; Arthur, Bull. Minnesota Acad. Sci., vol. 2, p. 15, 1883.

On *Hypericum anagaloides* Ch. and Sch., San Francisco, Olema, Mendocino County; on *H. Scouleri* Coulter, Amador County (Hansen).

Telia on Primulaceae

224. **Uromyces nevadensis** Hark. III
Bull. Calif. Acad. Sci., vol. 1, p. 36, 1884.

On *Primula suffrutescens* Gray, Lake Tahoe (Harkness). This collection was probably made in Nevada but very near the California boundary.

225. **Uromyces Armeriae** (Schl.) Lev. I, II, III
Ann. Sci. Nat., sér. 3, Bot., vol. 8, p. 375, 1847.

On *Armeria vulgaris* Willd., San Francisco, Pacific Grove (Heller).

Telia on Plumbaginacae

226. **Uromyces Limonii** (DC) Lév. I, II, III
Fl. franc., vol. 2, p. 195, 1805; Lev., Dict. d'hist. nat., p. 19, 1840.

On *Statice Limonium* L. var. *californicum* Gray, San Francisco, Belmont, Long Beach (Bethel).

Telia on Acanthaceae

227. **Uromyces Ruelliae** Holway. II, III
Ann. Mycol., vol. 2, p. 394, 1904.

On *Beloperone californica* Benth., western edge of the Colorado Desert, type of *Uredo Beloperonis* Arthur (Parish).

Telia on Compositae

228. **Uromyces Bidentis** Lagh. II, III
Bull. Soc. Mycol. France, p. 213, 1895.

On *Bidens pilosa* L., Orange; on *B. expansa* Greene, Long Beach (Bethel).

UROPYXIS schrot

Hedwigia, vol. 14, p. 165, 1875.

Uredinia erumpent, usually with paraphyses; urediniospores borne singly on pedicels. Telia erumpent; teliospores two-celled by a transverse septum; inner wall firm and deeply colored, outer wall gelatinous, thick.

229. **Uropyxis Amorphae** (Curt.) Schroet. II, III

Am. Jour. Arts and Sci., (2), vol. 6, p. 353, 1848; Hedwigia, vol. 14, p. 165.

On *Amorpha californica* Nutt., Mount Tamalpais and Los Gatos, Catalina Island (Bethel).

230. **Uropyxis sanguinea** (Peck) Arthur. II, III

Bot. Gaz., vol. 4, p. 128, 1879; N. A. Flora, vol. 7, p. 155.

On *Berberis pinnata* Leg., Berkeley; on *B. nervosa* Pursh., Humboldt County; on *B. repens* Lindl., Calaveras and Tuolumne counties.

ADDENDA

The following represent important additions to the foregoing list the data for which were received too late for inclusion in the proper sequence.

231. **Cronartium occidentale** Hedgcock, Bethel, and Hunt. 0, I, II, III

Jour. Agric. Research, vol. 14, p. 411, 1918.

Aecial stage not as yet reported from California but found in Colorado, Utah, New Mexico, and Arizona on species of *Pinus* belonging to the piñon group.

Uredinia and telia on *Ribes tenuiflorum* Lindl., "abundant along river wash near Monrovia" (Bethel). It was first reported from the same locality by W. M. Phillipson.

This record is of especial interest on account of the similarity of the uredinial and telial stages to those of the white pine blister rust, the aecial stage of which is very destructive to pines of the five-leaved group.

232. **Gymnosporangium inconspicuum** Kern. 0, I, III

Bull. Torr. Club, vol. 34, p. 461, 1907.

Aecia (*Roestilia Harknessianoides* Kern) on *Amelanchier* sp.

Telia on *Juniperus occidentalis* Hook. Both forms collected by Bethel in Bear River Valley, San Bernardino Mountains.

233. **Melampsora monticola** Mains. II, III

Phytopathology, vol. 7, p. 103, 1917.

Uredinia on *Euphorbia* sp., San Jose Cañon, near Carmel (Holway); on *E. leptosera* Engelm., Pacific Grove (Mrs. Clemens).

234. **Puccinia Andropogonis** Schw. 0, I, II, III
Trans. Am. Phil. Soc., II, vol. 4, p. 295, 1834.

Aecia on *Penstemon Menziesii* Hook., Yosemite Valley and Lake Tahoe.

Telia not reported from California, but to be expected on species of *Andropogon*.

235. **Puccinia Toumeyi** Sidow. III
Saccardo, Sylloge Fung., vol. 16, p. 299, 1902.

On *Penstemon spectabilis* Thurber, Mount Lowe.

236. **Puccinia yosemitana** Blasdale, sp. nov. I, III

Aecia usually solitary and widely scattered, cylindrical, about 0.2 mm. wide and 2.0 mm. long, orange yellow; pseudoperidia of thick-walled cells with deeply-colored contents, finally dehiscing by disintegration at apex.

Telia associated with aecia, amphigenous, scattered but occasionally confluent, about 0.5 mm. long, elliptical, black, pulverulent, early naked; teliospores ellipsoid or oblong, rounded and but slightly thickened at apex, barely constricted at septum, smooth, 32–38 by 20–22μ; pedicel thick, persistent, often 80μ long.

On *Gilia pungens* var. *Hookeri* Gray, found on trail from Yosemite Valley to top of Yosemite Falls.

237. **Pucciniastrum Galii** Fischer
Ured. d. Schweitz, p. 471, 1904.

Uredinia on *Galium triflorum* Michx. Yosemite Valley.

3. **Aecedium Trigochinis** Diet. and Holway

It has been shown very recently by Bethel that this is one of the many forms representing the aecial stage of *Puccinia submitens*.

67. **Puccinia sejuncta** Sydow.

It is now known that the form referred to under this number is *Aecidium Columbiense* Ell. and Ev. (Erythea, vol. 1, p. 206, 1893).

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A RUBBER PLANT SURVEY

OF

WESTERN NORTH AMERICA

I. CHRYSOTHAMNUS NAUSEOSUS AND ITS VARIETIES
HARVEY MONROE HALL

II. CHRYSIL, A NEW RUBBER FROM CHRYSOTHAMNUS NAUSEOSUS
HARVEY MONROE HALL AND THOMAS HARPER GOODSPEED

III. THE OCCURRENCE OF RUBBER IN CERTAIN WEST AMERICAN SHRUBS
HARVEY MONROE HALL AND THOMAS HARPER GOODSPEED

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I. *CHRYSOTHAMNUS NAUSEOSUS* AND ITS VARIETIES

BY

HARVEY MONROE HALL

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I. INTRODUCTION AND ACKNOWLEDGMENTS

In the course of an investigation of *Chrysothamnus* as a possible source of rubber, it has been found necessary to give considerable attention to the botanical relationships of the species and varieties of this genus of shrubs. Even before that investigation was begun in 1917, the author had undertaken a revision of the group and although the preparation of this has been delayed by the rubber studies it is intended now to carry it forward to completion. In the meantime, however, it is necessary that the forms discussed in the rubber report be properly defined and that those not hitherto recognized be named and described. These are the reasons for the publication of this preliminary paper.

Chrysothamnus is a genus of the Aster Tribe of the Compositae and belongs to what is often called the Haplopappus group. From related genera it differs chiefly in the more cylindraceous involucre, the bracts of which are usually more or less keeled and tend to fall into five vertical ranks. Although these characters are too variable to give to the genus that sharpness of delimitation that one would like, yet there can be no question as to its homogeneity. It represents what

is perhaps the most satisfactory result of all of the numerous attempts to set up genera in this group where generic limits are admittedly most difficult to establish.

Within the genus we find a multitude of natural forms of greater or less significance. This has led botanists greatly to increase the number of species and varieties, so that not less than one hundred and thirteen of these have been described and this number could be multiplied several times through more extensive field studies and without the employment of characters other than those already proposed for the basis of species. This is partly because these single characters have been variously united in nature to form a large number of combinations, but it is also because of the extreme variability of some of the characters themselves. The numerous forms of *Chrysothamnus* may be assembled into five natural groups as follows:

KEY TO THE SECTIONS OF *CHRYSOTHAMNUS*

Herbage not resinous-punctate: leaves oblanceolate to narrowly linear or terete.
  Heads in leafy spike-like or raceme-like clusters: outer bracts of the involucre prolonged into a slender herbaceous tip or appendage ..... Section 1. Parryani
  (Principal species: *Parryi, Howardi.*)
  Heads cymose, paniculate, or solitary at the ends of the branches: bracts obtuse to acuminate, devoid of herbaceous tip.
    Twigs not tomentose, either smooth and glabrous or only scabrid or puberulent: style-appendages from included to long-exserted.
      Bracts strongly keeled, in five very distinct vertical ridges ..... Section 2. Pulchelli
      (Principal species: *pulchellus, depressus.*)
      Bracts scarcely keeled and the vertical ridges obscure.. Section 3. Typici
      (Principal species: *albidus, Greenei, gramineus, Vaseyi, viscidiflorus.*)
    Twigs closely covered with a pannose tomentum which usually persists for several years: style-appendages mostly longer than the stigmatic portion and long-exserted ..... Section 4. Nauseosi
    (Single species: *nauseosus.*[1])
Herbage resinous-punctate: leaves terete ..... Section 5. Punctati
  (Principal species: *teretifolius, paniculatus.*)

Of the above five groups rubber has been found in more than minute quantities only in the *Nauseosi* and *Punctati*. Since the latter

[1] It is possible that *C. formosus* Greene and *C. turbinatus* (M. E. Jones) Rydb. constitute additional species of this group. See p. 180.

of these groups comprises only two species, and since these two species are already well defined in the literature and are not inclined to break up into numerous variants in nature, it is at the present time necessary to consider only the *nauseosus* group.

Taking *Chrysothamnus nauseosus* as comprising all of the forms of the *Nauseosi*, as indicated in the above key, we find its best distinguishing character to be the presence of a most remarkable pannose tomentum on the young twigs. It is fully recognized that pubescence characters often furnish but a very treacherous basis for constant species, yet in this instance the nature of the pubescence is so unlike that in any other species of the genus, and it is so obviously correlated with habit and other minor characters that it seems certainly to indicate a natural group. This felt-like covering to the twigs is more or less infiltrated with a resinous substance. In some forms the surface is loose and fluffy, the tomentum thus more or less completely masking the striae of the stems. In these forms the surface is usually light gray or dull white or even almost pure white, and the loose tomentum extends even to the involucres. The original *C. nauseosus* is one of these forms. In other varieties the surface of the tomentum is firm and smooth, thus revealing the striae. In these forms the twigs are dull to bright yellowish green in color or rarely somewhat whitish and the involucres are mostly glabrous.

Within what is here included under *C. nauseosus*, previous writers have described forty forms, all but six of which have been accorded specific rank at one time or another. In the present paper two new varieties are added. Nothing can be more certain than that these forty-two attempts to recognize species and varieties do not by any means exhaust the resources of the group. Every autumnal excursion into a new district brings to light one or more forms not previously described. The only limits set to the number of new species or varieties which might be set up lie in one's ability to visit all parts of the field during the flowering period and the failure or disinclination to recognize minute variations. Yet the systematist should include in his ultimate object not only the recognition of this multitude of forms but also their proper arrangement in a scheme which will display their natural relationships. Since this would entail an enormous amount of detailed labor, including extensive experiments, and since the results, even if attainable, would be of but little practical value at the present time, the writer has satisfied himself with the acceptance of twenty-two forms, all of which are treated as varieties.

This is believed to provide for all of the principal forms, and it is quite certain that each of the described varieties is a natural unit, although in most cases it is itself made up of still smaller variants.

Although the relationships between the varieties accepted in this paper are expressed somewhat in the arrangement, and in the form of brief notes from time to time, yet our actual knowledge of these matters is so slight that it seems unwise to attempt an expression of it through an elaborate system of polynomials. Some of the varieties are based upon characters which are at least partially heritable, while others are doubtless ecologic forms. In some cases two varieties occupying the same territory may be easily distinguished by a number of characters which at that locality do not overlap in their variations; yet as forms from other places are brought into comparison, it is discovered that these characters are so variable that they cannot be used for the recognition of species in the broad sense. It seems almost certain that after all of the forms shall have been assembled it will be found that no two of the characters thus far proposed for the separation of "species" in this group will be found to vary in unison, and furthermore that there is not a single one of them that does not vary by imperceptible degrees. Therefore we need not be surprised ultimately to find as many forms as there are possible combinations of characters and to have, in addition, numerous forms which cannot be satisfactorily placed because of the intermediate nature of one or more of the characters. It is thus seen to be impossible to accord specific rank to any of the units of this exceedingly complex and variable assemblage of forms unless one is willing to accept a species concept so narrow that its usefulness would be lost because of the impossibility of definite application.

If some readers object to the use of even trinomials we would suggest that the binomial indicating the inclusive major species, that is, *Chrysothamnus nauseosus* in this case, is all that need be used in most instances, while in any special paper on the group the varietal name alone may be used without confusion, since the generic and specific names are understood. This practice will be followed in the report on *Chrysothamnus* as a possible source of rubber, in which paper the actual working out of the method may be observed.

In preparing the following synopsis, the presence or absence of hairs on the involucre is taken as the principal character, notwithstanding its variable nature. This is done because it comes the nearest to assembling the forms into what seem to be natural groups, or sub-

species. Every other character tried, such as size or shape of the leaves or of the parts of the involucre or flower, the nature of the pappus or style-branches, and the pubescence of the akenes, have all been found to be even more variable and not to serve well as a basis for a natural classification. Moreover, the pubescent involucre is nearly always associated with a white or grayish appearance of the foliage so that the use of this character divides the whole species into two series of varieties, which series may, for the most part, be recognized by their general appearance.

After the foregoing remarks as to the variability of characters in this species it will perhaps be understood that one cannot expect to use the key to varieties with entire satisfaction. The large number of intermediate forms and the numerous permutations of characters render it impossible to prepare a key whereby one may definitely identify every specimen that comes to hand. It is believed, however, that with the exception of one or two little-known forms of eastern Oregon and Washington, all of the major variants have been accounted for.

This study has been greatly facilitated through the assistance of a considerable number of people but since these will be specifically mentioned in the report on the rubber plant investigations the list need not be given here. Acknowledgment should be made at this place, however, of the kindness of Dr. B. L. Robinson, of the Gray Herbarium of Harvard University, and also of that of Dr. P. A. Rydberg, of the New York Botanical Garden, in permitting the author to examine certain type specimens in their charge. Furthermore, Dr. Aven Nelson has made available the rich collections of the Rocky Mountain Herbarium at the University of Wyoming.

II. KEY TO THE VARIETIES OF *CHRYSOTHAMNUS NAUSEOSUS*[2]

Series A. The Gray Forms

Involucres tomentulose (at least the short outer bracts) to densely woolly: foliage mostly gray or even white with a rather copious pubescence, this either fine and close or floccose-tomentose (least pronounced in *oreophilus* and *speciosus*).

Akenes densely strigose.

Tomentum loose, copious, and nearly pure white on twigs and leaves, extending to the involucres: corolla-tube nearly always arachnoid-pubescent.

[2] See also doubtful forms on p. 180.

Inner bracts of involucre plainly tomentose or if nearly glabrous the bracts then acute.

Corolla-lobes lanceolate, 1 to 2 mm. long: involucral bracts acute (at least in part) ..... 1. *nauseosus* s. str.

Corolla lobes short ovate, less than 1 mm. long: bracts all very obtuse. 2. *hololeucus*

Inner bracts smooth and glabrous or nearly so, very obtuse ..... 3. *latisquameus*

Tomentum close, compact, smooth, and usually grayish on twigs and leaves: corolla-tube glabrous or puberulent, not arachnoid-pubescent.

Leaves 3 to 6 mm. wide: bracts very obtuse ..... 4. *salicifolius*

Leaves less than 3 mm. wide: bracts various but mostly acute.

Bracts abruptly acute. Far western ..... 6. *occidentalis*

Bracts gradually acute or somewhat obtuse.

Involucre 7 to 9 or rarely 10 mm. high.

Shrubs normally 5 to 20 dm. high: corolla 8 to 10 mm. long or rarely only 7 mm. in *gnaphalodes* (*latisquameus* of Arizona and New Mexico, with broad and very obtuse and smooth inner bracts might be sought here).

Leaves of flowering twigs 1 to 3 cm. long, not numerous: herbage usually fragrant ..... 5. *gnaphalodes*

Leaves of flowering twigs mostly over 3 cm. long, often crowded: herbage not fragrant ..... 7. *speciosus*

Shrubs only 2 to 6 dm. high: corolla 6 to 8 mm. long (very rarely 9 mm.).

Leaves erect or ascending: bracts all tomentulose or ciliate.. 8. *frigidus*

Leaves spreading or recurved: only the outer bracts tomentulose. 9. *plattensis*

Involucre 11 to 12 mm. or rarely only 10 mm. high ..... 10. *bernardinus*

Akenes glabrous.

Bracts of the involucre acuminate ..... 11. *Bigelovii*

Bracts of the involucre obtuse ..... 12. *glareosus*

Series B. The Green Forms

Involucres perfectly glabrous although sometimes viscidulous or glandular: foliage mostly greenish, the tomentum rather sparse or wanting on mature leaves.

Akenes glabrous ..... 13. *leiospermus*

Akenes densely strigose.

Leaves linear, mostly more than 1 mm. wide,[3] mostly 3 to 5-nerved except in *bernardinus*.

Involucre 6 to 8 mm. long: corolla 6 to 9 mm. long; lobes 1 mm. or less long ..... 14. *graveolens*

Involucre 9 mm. or more long: corolla 9 to 10 mm. long; lobes 1 mm. or more long. Western forms.

Heads 8 to 10 flowered: leaves flat or twisted, 2 to 5 mm. wide. 15. *californicus*

Heads 5-flowered (rarely 6-flowered): leaves often conduplicate, 1 to 2 mm. wide ..... 10. *bernardinus*

Leaves linear-filiform or very narrowly linear, mostly 1 mm. or less wide (except in *occidentalis*), 1-nerved.

[3] Care must be exercised in making this measurement since the leaves are often longitudinally folded. The figures given are for the total width of the flat leaf.

Bracts of the involucre abruptly pointed or some only acute. Far western.
Tip of the bract short, erect ..... 6. *occidentalis*
Tip of the bract about 1 mm. long, very slender, recurved 16. *ceruminosus*
Bracts obtuse to acute, not abruptly pointed.
Corolla-lobes glabrous.
Involucre 6 to 9 mm. long, not sharply angled.
Bracts ciliate, the outer often slightly hairy also on back, flat, thin, scarcely keeled ..... 17. *oreophilus*
Bracts not ciliate, all perfectly glabrous, concave, somewhat keeled.
Corolla 7 to 8.3 mm. long; lobes under 2 mm.: twigs and foliage slender.
Lobes of corolla 0.5 to 1 mm. long, rarely more: inflorescence typically rounded to pyramidal. Rocky Mountain states. 18. *pinifolius*
Lobes of corolla 1 to 2 mm. long: inflorescence typically cylindric to pyramidal. Great Basin ..... 19. *consimilis*
Corolla 8 to 10 mm. long; lobes 1.7 to 2.5 mm. long: twigs and foliage stouter. Southwestern ..... 20. *viridulus*
Involucre 9 to 10 mm. long, sharply 5-angled, the strongly keeled bracts in very distinct vertical rows ..... 21. *mohavensis*
Corolla-lobes sparsely long-hairy in the bud: shrub nearly leafless. 22. *junceus*

III. SYNOPSIS OF THE VARIETIES OF *CHRYSOTHAMNUS NAUSEOSUS*

1. **Chrysothamnus nauseosus** (Pall.) Britt. (*sensu strictu*) *in* Britt and Br., Ill. Fl., vol. 3, p. 326, 1898.

Chrysocoma nauseosa Pall., *in* Pursh, Fl., vol. 2, p. 517, 1814.
Chrysothamnus speciosus albicaulis Nutt., Trans. Am. Philos. Soc., ser. 2, vol. 7, p. 324, 1841.
Bigelovia graveolens albicaulis Gray, Proc. Am. Acad., vol. 8, p. 645, 1873.

Shrub 5 to 10 dm. high, with numerous erect or ascending twigs, leafy to the top, permanently white-tomentose throughout; twigs not evidently striate: leaves narrowly linear, 3 to 6 cm. long, 0.5 to 1.5 mm. wide: inflorescence a rather loose round-topped cyme: involucre 7 to 8 mm. high; bracts mostly acute, plainly keeled, in 5 distinct vertical ranks, white-woolly but not ciliate: corolla 7.5 to 9 mm. long; tube perhaps always cobwebby with long weak hairs; lobes lanceolate, 1 to 2 mm. long.

This type form of the species is much less common than many of its varieties. It occurs from Utah to Oregon and probably north to British Columbia and Montana, inhabiting well drained soil with little or no alkali. In the typical form, as understood by the writer, the leaves are very narrow and, like the twigs, are entirely covered with a white flocculent tomentum, while the corolla-tube is conspicu-

ously arachnoid-pubescent. Such are specimens gathered by Leiberg in eastern Washington under no. 884 and others by Marcus E. Jones at Marysvale, Utah, under no. 5968. In northern Mono County, California, is encountered a form in which the leaves are 2 to 3 mm. wide and the inflorescence is more compact and rounded (H. M. H., no. 463), but in the pubescence of the corolla-tube and in all other characters than those mentioned it is plainly *nauseosus*. Nearly identical are specimens from Truckee, California (Heller, no. 7192). Another divergence is indicated by specimens with the broad leaves and other characters of the Mono and Truckee collections just cited but with a corolla-tube which is only crisp-pubescent as in most varieties. A recognition of these forms would lead only to confusion since further field studies would doubtless reveal still other divisions that might be made. They are therefore retained in this paper as only trivial variants of *nauseosus*. *C. orthophyllus* Greene, Pitt., vol. 5, p. 62, 1902, known only from Plumas County, California, is described as less than a foot high and with the tips of the corolla-lobes as well as the tube long-villous.

2. **Chrysothamnus nauseosus** var. **hololeucus** (Gray) comb. nov.

Bigelovia graveolens var. *hololeuca* Gray, Proc. Am. Acad., vol. 8, p. 645, 1873.

Shrub 6 to 18 dm. high and fully as broad, closely branched and usually of rounded outline, leafy throughout: herbage exceedingly fragrant, densely clothed with a nearly pure white tomentum which completely masks the striae of the stem and extends even to the involucres: leaves 1 to 3 cm. long, about 1 but sometimes nearly 2 mm. wide: inflorescence a rounded often compact cyme: involucre 6 to 7 mm. high; bracts very obtuse, plainly keeled and in 5 distinct vertical ranks, woolly but not ciliate: corolla 6.5 to 8 mm. long; tube more or less cobwebby with loose hairs or these occasionally wanting; lobes ovate, acute, strictly erect, 0.5 to 1 mm. long.

The type of *hololeucus* came from Owens Valley, California, whence we now have collections from a number of stations. What appears to be the same form occurs as far south as Antelope Valley and very good *hololeucus* grows as far north as Pyramid Lake, Nevada, but it does not have a wide east-and-west range. It is confined to loose gravelly or sandy well drained slopes and even in such places it never forms pure stands but occurs as scattered individuals among bushes of other sorts, commonly *C. n. gnaphalodes* and *Artemisia tridentata*. The plants are so white in comparison with these other shrubs that they can be distinguished in the field without difficulty.

3. **Chrysothamnus nauseosus** var. **latisquameus** (Gray) comb. nov.

Bigelovia graveolens latisquamea Gray, Proc. Am. Acad., vol. 8, p. 645, 1873.

Shrub tall (perhaps rounded at top), leafy to summit: herbage white with a rather loose tomentum: leaves 2 to 5 cm. long, less than 1 mm. wide: inflorescence a loosely branched rounded compound cyme: involucre about 8 mm. high (7 to 9 mm.); bracts carinate, about 4 in each of the 5 distinct vertical rows, outermost ones tomentulose, inner ones very obtuse and usually glabrous: corolla about 9 mm. long; tube short-pubescent or glabrous; lobes ovate or short-lanceolate, 0.4 to 0.9 mm. long, erect.

A common variety of New Mexico and Arizona. *Bigelovia graveolens appendiculata* Eastw., Proc. Calif. Acad. Sci., ser. 3, vol. 1, p. 74, 1897, from the White Sands of New Mexico, is an abnormal form with one to four linear appendages on the corolla-tube. The tube is arachnoid-pubescent and the lobes are only about 0.4 mm. long, both of which characters suggest an affinity with *hololeucus*. *C. arizonicus* Greene, Pitt., vol. 4, p. 42, 1899, is a form with the corolla-tube "cleft rather deeply." The type is from the Santa Rita Mountains.

4. **Chrysothamnus nauseosus** var. **salicifolius** (Rydb.) comb. nov.

Chrysothamnus salicifolius Rydb., Bull. Torrey Club, vol. 37, p. 130, 1910.

Shrub 3 to 10 dm. high, with erect branches: leaves 3-nerved, 4 to 8 cm. long, 3 to 6 mm. wide, minutely tomentulose: inflorescence cymose, dense: involucre 7 to 8 mm. high; outer bracts slightly tomentulose, the inner glabrous and very obtuse: corolla about 10 mm. long; lobes 1.5 to 2 mm. long.

Apparently a rare variety and confined to Utah; known to the writer from only two collections, namely, Strawberry Valley, at 7000 feet altitude, F. E. Leonard, no. 288 (type), and near Salt Lake City, A. O. Garrett, no. 2455.

5. **Chrysothamnus nauseosus** var. **gnaphalodes** (Greene) comb. nov.

Chrysothamnus speciosus var. *gnaphalodes* Greene, Eryth., vol. 3, p. 110, 1895.

Shrubs 5 to 15 or rarely 25 dm. high, usually globoid in outline, with very many short twiggy branches, not densely leafy: herbage very fragrant, gray with a closely packed tomentum, the twigs obscurely striate: leaves 2 to 4 mm. long, 1 mm. or less wide, those of the end twigs only 1 to 3 cm. long and often recurved: inflorescence a rounded cyme terminating each of the twigs: involucre about 7 mm. high; bracts rather obtuse, keeled, in 5 distinct vertical rows, tomentose, not ciliate: corolla 7 to 8 mm. long; tube sparsely pubescent with short crisp or rigid hairs; lobes ovate, acute, erect or even connivent around the stamen-tube, 0.5 to 1 mm. long.

This is the common gray variety of gravelly or sandy non-alkaline slopes and benches of western Nevada and eastern California from Pyramid Lake south to the Cajon, Soledad, and Tehachapi passes, and to Arizona. It belongs especially to the loose soil of well drained slopes surrounding valleys the alkaline bottoms of which are occupied by *viridulus*, and often forms belts of considerable extent. It is the most common shrub on land from which sagebrush has been burned or otherwise cleared, and is subclimax to that abundant shrub.

6. **Chrysothamnus nauseosus** var. **occidentalis** (Greene) Hall
Univ. Calif. Publ. Bot., vol. 3, p. 60, 1907.

Chrysothamnus californicus occidentalis Greene, Eryth., vol. 3, p. 112, 1895.

Shrub probably rather low, with numerous short slender erect branches, the leafy stems gray-tomentose but not loosely or flocculently so; leaves narrowly linear, 4 cm. or less long, mostly less than 1 mm. wide, but occasionally up to 2 mm., 1-nerved, tomentulose; inflorescence compactly cymose, rounded, 2 to 5 cm. across; involucre 7 to 9 mm. high; at least some of the bracts abruptly acute or cuspidate, the outer ones more or less glandular-puberulent; corolla 8 to 9 mm. long; lobes lanceolate-linear, 1.7 to 2.5 mm. long.

The distribution of this variety was originally stated by Greene to be "In the Coast Range, from Humboldt County (California) southward." Later, this same author stated it as "Kern and Santa Barbara counties."[4] This restriction in the adopted range was perhaps due to the fact that certain specimens from Humboldt and other northern counties do not meet the requirements of the description as well as those from further south. The cuspidate bracts and long corolla-lobes, together with the habit (especially the small compact rounded inflorescence), are here taken as the most satisfactory characters for the variety. Accepting this definition, we find fairly typical collections from the dry inner north Coast Ranges and from the southern Sierra Nevada and San Bernardino Mountains. North and east of Trinity County it apparently passes into *speciosus*, from which it scarcely differs save in the more nearly glabrous and abruptly pointed bracts. At its southernmost stations it meets and perhaps merges into *bernardinus*.

The following are taken as typical: near summit of South Yolla Bolla, Trinity(?) County, October, 1916, Merriam and Bailey; Little Kern River, Tulare County, C. A. Purpus, no. 2040; Barton Flats, in the San Bernardino Mountains, Mrs. Wilder, no. 597 (corolla up

[4] Greene, Fl. Fr., 1897, p. 369.

to 10 mm. long). *C. tortuosus* Greene, Pitt., vol. 5, p. 63, 1902, is aparently a form intermediate between this and *speciosus*. It is described as having tortuous flowering branches, nearly filiform more or less spreading leaves which are also tortuous, and rather pungently acute bracts. The types came from Plumas County and Mount Shasta, California.

7. **Chrysothamnus nauseosus** var. **speciosus** (Nutt.) comb. nov.

Chrysothamnus speciosus Nutt., Trans. Am. Philos. Soc., ser. 2, vol. 7, p. 323, 1841.

Shrub commonly 6 to 20 dm. high, broad and rounded, leafy to summit: twigs greenish white, the tomentum comparatively thin and smooth: leaves 2 to 6 cm. long, typically about 1 mm. wide but varying to 3 mm., usually erect or ascending, becoming dense towards the inflorescences and there scarcely reduced in size, gray, tomentose or the tomentum partly deciduous and the foliage then greenish: inflorescence a round-topped or somewhat elongated cyme, commonly loose: involucre 7 to 10 mm. high; bracts 3 or 4 in each row, acute, concave, tomentulose on the back, not ciliate: corolla 8 to 10 mm. long; tube sparsely puberulent or glabrous; lobes 0.8 to 2 mm. long.

The above description is drawn to include a number of forms. In this broad sense *speciosus* has a range from Idaho and Utah to California and Washington. It is a variety belonging to sandy slopes and benches with little or no alkali. The type came from "the Rocky Mountain plains, near Lewis River" and was described as having narrow, linear, acute, more or less tomentose leaves and heads in dense, conglomerate, terminal clusters. A form which answers to this but with a slightly elongated and loose inflorescence is common from northern Utah to eastern Oregon and northern California where, through the nearly glabrous character of the involucre it passes into *occidentalis*. Further south in eastern California and western Nevada the involucre becomes more compact and nicely rounded but in this form the comparatively rigid leaves are 2 to 3 mm. wide and vary from gray to yellowish green. This type was apparently included by Dr. Greene in his *californicus*. In the absence of better characters and with our scant knowledge of the real *speciosus* it seems unwise to segregate these forms more definitely at present, although they are more striking than many of the Rocky Mountain varieties accepted in this paper. *C. pulcherrimus*, A. Nels., Bot. Gaz., vol. 28, p. 370, 1899, is a form of the high plains of the Rocky Mountain states, especially in moist soil. All of the characters used to differentiate it from *speciosus* are variable and no two of them vary in unison, but

the more nearly glabrous nature of the involucre seems to be the most important. As pointed out by Dr. Nelson, it also resembles *graveolens*, but the narrower leaves are constantly one-nerved and the involucre is not absolutely glabrous. *C. pulcherrimus fasciculatus* A. Nels., l.c., is described as having numerous short branchlets and numerous rigid leaves only 2 to 3 cm. long. It has been collected at Boulder Creek and at Creston, both of these localities being in Wyoming.

8. **Chrysothamnus nauseosus** var. **frigidus** (Greene) comb. nov.

Chrysothamnus frigidus Greene, Eryth., vol. 3, p. 112, 1895.

Sub-shrub woody only at the base, often nearly prostrate, 2 to 6 dm. high, with mostly erect stems, very leafy: twigs whitish with a smooth close tomentum: leaves 2 to 5 cm. long, 1 to 1.5 mm. wide, mostly erect or ascending, white-tomentose: inflorescence cymose or elongated: involucre about 7 mm. high; bracts tomentulose and somewhat glandular, ciliolate at least at summit: corolla 6 to 7 mm. long; tube puberulent; lobes linear-lanceolate, 1.2 to 1.5 mm. long.

This variety belongs to the elevated bleak plains of the Rocky Mountain states, is especially common on the Wyoming plateaus, and is said to occur as far north as Alberta. In one collection (Aven Nelson, no. 2787, from Laramie) the corolla-tube is well provided with a long loose cobwebby pubescence, just as in the otherwise very different *nauseosus* proper and in *hololeucus*. *C. frigidus concolor* A. Nels., Bot. Gaz., vol. 28, p. 371, 1899, is a form with yellowish green herbage and somewhat elongated inflorescences. It grows in sandy more or less alkaline soil in Wyoming and Montana. *C. pallidus* A. Nels., l.c., p. 372, is a form also allied to *frigidus* and perhaps to be united with it. The twigs are less leafy except near the top, where they are shorter and more crowded; the herbage is nearly white with a close persistent tomentum. It inhabits alkaline soil in Wyoming and northern Colorado.

9. **Chrysothamnus nauseosus** var. **plattensis** (Greene) comb. nov.

Chrysothamnus speciosus(?) plattensis Greene, Eryth., vol. 3, p. 111, 1895.

Characters as given for *frigidus* except that the narrower leaves are loosely spreading or even recurved and that only the outer bracts are tomentulose.

A form of the alkaline plains along the eastern base of the Rocky Mountains. The type was described as having rather densely woolly-ciliate bracts but in most collections the bracts are only obscurely

ciliate. Since also the direction assumed by the leaves is not constant, this variety is exceedingly unstable and probably represents an ecologic form.

10. **Chrysothamnus nauseosus** var. **bernardinus** var. nov.

Shrub leafy to the summit: annual twigs strict, about 3 dm. long, coated with a smooth gray pannose tomentum, not striate: leaves ascending, linear, 3 to 5 cm. long, 1 to 2 mm. wide, mostly conduplicate, 1-nerved, very acute, often recurved at tip, green and scabro-puberulent: inflorescence a loose rounded cyme, 3 to 5 cm. across, the lower branches 2 to 6 cm. long: involucre 5-flowered, cylindric-turbinate, about 12 mm. high; bracts in well-defined ranks, 4 in each rank, keeled, thin, stramineous, lanceolate (the short outermost ones ovate), sharply acuminate, glabrous or slightly erose-ciliate or the outer ones obscurely puberulent: corolla 9 to 10 mm. long; tube sparsely crisp-puberulent; lobes linear-lanceolate, acute, 1.8 to 2 mm. long: anther-tips acute, about 0.5 mm. long: style-branches about 4 mm. long, stigmatic about one-half their length: akenes densely sericeous-pubescent: pappus soft, about 8 mm. long, becoming pink.

Frutex undique foliosus: ramulis horotinis strictis non striatis, ca. 3 dm. longis, tomento pannoso cinereo vestitis: foliis ascendentibus, linearibus, 3–5 cm. longis, 1–2 mm. latis, plerumque complicatis, 1-nerviis, acutissimis, apice saepe recurvatis, viridis, scabro-puberulis: inflorescentia cymam rotundam laxifloram formante, 3–5 cm. latam, ramulis inferioribus 2–6 cm. longis: involucris 5-floris, cylindrato-turbinatis, ca. 12 mm. altis, squamis distincte seriatis in utraque serieri verticali 4, carinatis, tenuibus, stramineis, lanceolatis (exterioribus brevioribus ovatis), acuminatis, glabris, nunc parce eroso-ciliatis nunc exterioribus obscure puberulis: corolla 9–10 mm. longa; tubo parum crispo-puberulo; lobis lineari-lanceolatis, acutis, 1.8–2 mm. longis: antheris apice acutis, ca. 0.5 mm. longis: styli ramis ca. 4 mm. longis, parte stigmatice duplo longioribus: achaeniis dense sericeo-pubescentibus: pappi setis tenuibus, ca. 8 mm. longis, colore deinde roseis.

Dry, open hillside at 7400 feet altitude, Bluff Lake, San Bernardino Mountains, California, September 2, 1905, Joseph Grinnell (Herb. Univ. Calif. no. 149208), type. As far as known, this variety is confined to the San Bernardino and San Antonio mountains of southern California. The specimens cited below exhibit the following variations: cyme up to 10 cm. in diameter and the lower branches 10 cm. long: involucre 10 to 13 mm. high, occasionally six-flowered. Because of the frequent longitudinal folding of the leaves, these structures often appear much narrower than they really are. This applies to the type as well as to most of the other specimens cited.

In addition to the type, the following collections apparently belong here: Little Bear Valley, San Bernardino Mountains, Mrs. C. M. Wilder, no. 740; Little Green Valley, San Bernardino Mountains,

Geo. R. Hall, no. 34; Pine Mountain Ridge, San Antonio Mountains, I. M. Johnston, no. 1652; rocky hillsides of Round Valley, San Jacinto Mountain at 9000 to 9500 feet altitude, H. M. Hall, no. 341. In this last mentioned collection the compact cymes are only 3 to 4 cm. across, the anther-tips are 1 mm. or more long and very slender, the style-branches are fully exserted and 4 to 6 mm. long. A detailed study of fresh material may demonstrate that it is a variety distinct from *bernardinus*, but the specimens at hand are too meagre to justify this.

The variety *bernardinus* is somewhat like *occidentalis* but with a larger and looser inflorescence, longer involucres and flowers, and thinner tegules which are gradually acuminate instead of abruptly pointed. In most of its characters, as well as in the appearance of herbarium specimens it almost duplicates the Rocky Mountain *pulcherrimus*, here referred to var. *speciosus*, but the involucre is longer and the more strongly keeled bracts are acuminate instead of merely acute. Moreover the geographic isolation of *bernardinus* argues for its recognition as a variety distinct from *pulcherrimus*.

11. **Chrysothamnus nauseosus** var. **Bigelovii** (Gray) comb. nov.

Linosyris (*Chrysothamnus*) *Bigelovii* Gray, Pacif. R. R. Rept., vol. 4, no. 4, p. 98, 1857.

Shrub densely branched, 3 to 10 dm. high: twigs short, leafy, yellowish green with a closely packed tomentum: leaves linear-filiform, 1 to 3 cm. long, tomentulose when young: inflorescence a lax few-headed cyme terminating each of the branches: involucre 10 to 12 mm. high; bracts 4 or 5 in each row, tomentulose and sometimes ciliate, attenuate, spreading in age: corolla 8 to 9 mm. long; lobes ovate, erect, 0.5 to 0.8 mm. long: akenes glabrous.

The variety *Bigelovii* is a form from the very dry plains and hills of the southern Rocky Mountain region and southward to Texas. It has been classified near to *C. pulchellus* but the brittle striate twigs and divaricate branching of that species indicate for it an entirely different origin. Moreover, the loose involucres of *Bigelovii*, with bracts in only obscurely vertical ranks, are very unlike those of the *Pulchelli*. It is plainly a variant of *nauseosus*, and its nearest affinity will probably be found in var. *leiospermus*, from which it differs chiefly in the very pubescent and acute bracts. Specimens gathered in southeastern Utah by Rydberg and Garrett (nos. 9435, 9940) are intermediate, having the essentially glabrous involucres of *leiospermus* but with bracts which are almost as sharp as in *Bigelovii*.

12. **Chrysothamnus nauseosus** var. **glareosus** (M. E. Jones) comb. nov.

Bigelovia glareosa M. E. Jones, Zoe, vol. 2, p. 247, 1891.

Shrub many-stemmed, said to be only about 3 dm. high: leaves broadly linear, slightly widened above, plane: inflorescence cymose: bracts about 4 in each vertical row, somewhat keeled, obtuse, sparsely erose-ciliate, scurfy-tomentulose: corolla about 12 mm. long; lobes linear-lanceolate: akenes glabrous.

This variety is apparently restricted to central and southern Utah, where it grows on gravelly mesas. It was originally compared with *leiospermus*, from which it differs in the tomentulose involucre and other characters.

13. **Chrysothamnus nauseosus** var. **leiospermus** (Gray) comb. nov.

Bigelovia leiosperma Gray, Syn. Fl., vol. 1, part 2, p. 139, 1884.

Shrub low (3 to 12 dm. high), with numerous short erect twigs, these either moderately leafy or almost naked: twigs yellowish green with a very close tomentum: leaves filiform or nearly so, acute, mostly 0.5 to 2 or 3 cm. long, essentially glabrous: heads in close terminal cymes of 2 or 3 cm. diameter: involucre 6 to 8 mm. high: bracts linear-oblong except the short ovate outer ones, obtuse, glabrous: corolla 5 to 8 mm. long, the tube very obscurely pubescent (or glabrous?); lobes ovate, erect, glabrous, 0.5 mm. or less long: akenes completely glabrous in the typical form but often sparsely pubescent, especially along the prominent nerves.

This form inhabits the most arid portions of the Great Basin, growing mostly on very dry exposed hillsides or in dry rocky streamways. The only collections seen by the writer are from Clear Creek Cañon, Utah, Candelaria in western Nevada, and Caliente in eastern Nevada. The Clear Creek specimens formed the basis of *Bigelovia leiosperma* var. *abbreviata* M. E. Jones, Proc. Calif. Acad. Sci., ser. 2, vol. 5, p. 693, 1895, a form with scant tomentum and leaves 1 cm. or less long. The Caliente specimens (H. M. H., nos. 10791, 10795) represent an extremely xerophile type of very dry exposed hillsides in the Lower Sonoran Zone. Their stems are green and rush-like, and the leaves reduced to scales about 3 mm. long, or rarely developed and then about 1 cm. long. In one of the Caliente specimens the akenes are very sparsely pubescent on the edges; in another from the same station they are sparsely pubescent also on the intervals. This indicates that the absence of pubescence cannot be satisfactorily used as a specific character. The relationships of *leiospermus* are probably with *Bigelovii*.

14. **Chrysothamnus nauseosus** var. **graveolens** (Nutt.) Piper.
Contr. U. S. Nat. Herb., vol. 11, p. 559, 1906.

Chrysocoma graveolens Nutt., Gen., vol. 2, p. 136, 1818.
Bigelovia graveolens glabrata Gray, Proc. Am. Acad., vol. 8, p. 645, 1873.

Shrub robust, leafy to summit: twigs yellowish green to nearly white, more or less striate, the tomentum compact and smooth: leaves broadly linear, 1 to 3 mm. wide, mostly 3- or 5-nerved, impunctate, smooth and green but often slightly tomentulose, especially beneath: inflorescence a round or flat-topped cyme, fastigiate, the heads crowded: involucre 6 to 9 mm. high, glabrous: corolla 6 to 9 (rarely 10) mm. long; lobes 0.5 to 1 or rarely 1.6 mm. long, erect.

There can be little doubt that the original of Nuttall's *Chrysocoma graveolens* is the plant here described, for in the brief description are mentioned the linear, three-nerved, smooth leaves; the corymbosely fastigiate and crowded "flowers"; and the smooth, five-flowered, angular "calix." This is the common form in the easterly part of the range of the genus, especially in Wyoming, Colorado, and northern New Mexico. *C. virens* Greene, Pitt., vol. 5, p. 61, 1902, apparently is not to be retained even in the most subordinate rank. From the description it seems to be very near to *graveolens* but it is perhaps greener, the involucre only one-half as long as the flowers, and the bracts somewhat triangular. These characters are all extremely variable. Although the writer has searched for it at the type locality (Cañon City, Colorado) and in surrounding districts, no specimens were found that could be satisfactorily separated from *graveolens*. *C. laetevirens* Greene, l.c., described from material gathered at Grand Junction, Colorado, has been studied at its type locality. Apparently there is no reason for considering it more than a light-green form or state of *graveolens*.

15. **Chrysothamnus nauseosus** var. **californicus** (Greene) comb. nov.

Chrysothamnus californicus Greene, Eryth., vol. 3, p. 111, 1895, in part.

Shrub low and leafy-stemmed: twigs white with appressed tomentum, leafy to the summit: leaves broad (2 to 5 mm.), narrowly oblanceolate, 3-nerved, scarcely tomentulose but green and densely glandular: inflorescence minutely glandular, consisting of short terminal cymes: involucre 9 to 10 mm. high, 8 to 10-flowered: bracts thin, loose, only 2 or 3 in each vertical row, all lanceolate, attenuate, not tomentose but rather densely glandular: corolla about 10 mm. long; lobes 1.2 to 1.5 mm. long; tube puberulent (not arachnoid).

As here restricted, *californicus* is a rare sub-shrub of the high Sierra Nevada. Our description is drawn from Bolander's no. 6137 from Mono Pass at 9000 to 10,000 feet altitude. In the original description Greene combined with this a taller form with tomentulose leaves and inflorescence and 5-flowered heads, which form belongs to lower altitudes and is included in *speciosus* of the present synopsis.

16. **Chrysothamnus nauseosus** var. **ceruminosus** (Dur. & Hilg.) comb. nov.

Linosyris ceruminosa Dur. & Hilg., Pac. R. Rept., vol. 5, part 3, p. 9, pl. 6, 1856.

Shrub 5 to 12 dm. high, fastigiately branched, the stems yellowish green with a compact tomentum: leaves linear-filiform, 1 to 3 cm. long, tomentulose: inflorescence compactly cymose, rounded, 2 to 3 cm. across: involucre 7 to 8 mm. high; bracts thin, yellowish, abruptly narrowed to a filiform recurved mucro about 1 mm. long, glabrous and glutinous or apparently somewhat puberulent: corolla about 6.5 mm. long; lobes 1 to 1.7 mm. long.

Known from only two collections, namely, the type collection by Dr. Heermann somewhere near Tejon Pass, California, and one made by Mrs. Spencer in October, 1917, at Hesperia, a station on the Mojave Desert about ninety miles east of Tejon Pass.

17. **Chrysothamnus nauseosus** var. **oreophilus** (A. Nels.) comb. nov.

Chrysothamnus oreophilus A. Nels., Bot. Gaz., vol. 28, p. 375, 1899.

Shrub described as 2 to 4 dm. high with erect stems, very leafy to the top: twigs yellowish green, the tomentum thin and smooth: leaves 3 to 7 cm. long, about 1 mm. wide, strictly erect, the upper ones crowded and not reduced, all tomentulose at least when young but green: inflorescence composed of numerous small cymes in a more or less elongated but round-topped thyrse: involucre 7 to 8 mm. high; bracts carinate, acute, sparingly tomentulose, ciliolate: corolla 7 to 10 mm. long; tube crisp-pubescent; lobes linear-lanceolate, 1.3 to 2 mm. long.

This is an apparently rare plant of saline soils in Wyoming and Idaho. Its characters indicate that it may be a derivative of *graveolens* differing chiefly in the narrower leaves and much longer corolla-lobes. In the latter respect it resembles *consimilis*, into which more westerly form it probably intergrades. The more numerous and wider strictly erect upper leaves and the somewhat flat ciliate bracts may, however, serve to distinguish it from *consimilis*.

18. **Chrysothamnus nauseosus** var. **pinifolius** (Greene) comb. nov.

Chrysothamnus pinifolius Greene, Pitt., vol. 5, p. 60, 1902.

Shrub of medium size, with slender, very leafy stems: leaves linear-filiform, 1 mm. or less wide, 1-nerved, green to grayish puberulent, often densely tomentulose beneath: inflorescence a thyrsoid panicle of rounded or pyramidal outline, varying to short-oblong: involucre about 7 mm. long, glabrous: corolla 6 to 9 mm. long; lobes 0.5 to 1 mm. long.

Most abundant in Colorado but extending into adjacent states; replaced further west by *consimilis*. The characters separating this variety from *graveolens* seem to be correlated with the more vigorous growth of the latter and intermediate forms are common. *C. patens* Rydb., Bull. Torrey Club, vol. 31, p. 652, 1904, is a form of *pinifolius* with spreading and more or less falcate leaves, but this character is widely variable on single plants and moreover it does not vary in unison with other characters. The corolla-lobes in *pinifolius* are described as about 0.5 mm. long; those of *patens* as about 1 mm. long. However the lobes are not infrequently as much as 1 mm. long and occasionally even 1.4 mm. in plants otherwise typical of *pinifolius*. *C. confinis* Greene, Pitt., vol. 5, p. 62, 1902, of New Mexico, is scarcely separable from *pinifolius*. Its best characters lie in the rather obtuse and short-ciliate bracts, but even in *pinifolius* at least a portion of the bracts are more or less ciliate. *C. falcatus* Greene, l.c., based upon specimens collected on the plains about Grand Junction, Colorado, is *pinifolius* with the lower face of the leaves white-tomentose, as is commonly the case. Dr. Greene used also the curvature of the leaves and the angle made by them with the stem as differentiating criteria but field studies made by the author at Grand Junction indicate that such characters are much too variable, even in individual plants, to be of use. This is indicated by sheets nos. 203083 and 203177 at the University of California, under *graveolens*.

19. **Chrysothamnus nauseosus** var. **consimilis** (Greene) comb. nov.

Chrysothamnus consimilis Greene, Pitt., vol. 5, p. 60, 1902.

Shrub of medium or large size, the slender erect twigs very leafy: leaves ascending or spreading, nearly filiform, less than 1 mm. wide, 1-nerved, somewhat resinous and canescently tomentulose to nearly glabrous: inflorescence an elongated pyramidial or cylindric thyrsus: involucre 7 to mostly 8 or 9 mm. high: bracts not in distinct vertical rows, glabrous: corolla 7.3 to 8.3 mm. long; lobes 1 to 2 mm. long, spreading in age.

This is the common *Chrysothamnus* on alkaline flats of the Great Basin, especially in northern Nevada, whence it extends to Arizona, California, Oregon, and Idaho. In western Utah also it is the common alkali-flat form but easterly it merges both in characters and distribution into *pinifolius*. It may usually be distinguished from this form by the longer, more spreading corolla-lobes, and sometimes by the more elongated inflorescence. To the southwest of its range it passes into *viridulus*, as indicated under that variety. *C. angustus* Greene, Pitt., vol. 5, p. 64, 1902, described from specimens collected in northeastern California, is exactly the same. It was said to be distinguishable by its canescent "woolliness," but copious material from both type localities indicates that this character can be correlated neither with other characters nor with geographic distribution, and the amount of pubescence is of course variable. These remarks apply equally well to leaf-length, and no other differentiating characters appear in the descriptions.

20. **Chrysothamnus nauseosus** var. **viridulus** var. nov.

Shrub robust, green, about 1.5 m. high, leafy to the summit: twigs densely covered with pannose yellowish green tomentum, rather stout, striate: herbage malodorous: leaves at first erect or ascending, later inclined to droop, narrowly linear, 3 to 5 cm. long, about 1 mm. wide, acute, 1-nerved, channeled above, green but tomentulose on both sides: inflorescence a pyramidal to nearly globose thyrse: involucre 6 to 7 mm. high, glabrous but viscid with a resinous exudation; bracts 3 or 4 in each of the 5 vertical ranks, carinate, the outer ones acute, the innermost ones obtuse: flowers, 5: corolla 8.3 to 10 mm. long; tube glabrous or sparsely puberulent, passing gradually into the throat; lobes linear, acute, 2 to 2.5 mm. long, 0.4 mm. wide, recurving in age: anthers 3 to 3.3 mm. long, the tip 0.42 to 0.68 mm. long: akenes densely sericeous: pappus about 7.5 mm. long.

Frutex validus, viridis, ca. 15 dm. altis, undique foliosus: ramulis tomento luteolo-viridi dense vestitis, paullo robustis striatis, odore injucundis: foliis primum erectis vel ascendentibus, deinde flaccescere inclinantibus, anguste linearibus, 3–5 cm. longis, ca. 1 mm. latis, acutis, 1-nerviis, supra impressis, viridulis, utrinque tomentulosis: inflorescentia thyrsum globoso-pyramidatum formante: involucro 6–7 mm. alto, glabro, resinoso-viscido: squamarum seriebus verticalibus 5, in utraque serieri 3–4, carinatis, exterioribus acutis, interioribus obtusis: floribus 5: corolla 8.3–10 mm. longa, tubo glabro parce puberulo, infundibuliformi, lobis linearibus, acutis, 2–2.5 mm. longis, 0.4 mm. latis, deinde recurvatis: antheris 3–3.3 mm. longis mucrone 0.42–0.68 mm. longo: achaeniis dense sericeis: pappo ca. 7.5 mm. longo.

Benton, Mono County, California, on sandy alkaline flats with *Distichlis*, in the Upper Sonoran Zone, at 5640 feet altitude, Novem-

ber 3, 1917, H. M. H., no. 10642 (Herb. Univ. Calif. no. 203068), type. This is the common form on alkaline flats in southern Mono County and in Inyo County, California, and in western Esmeralda County, Nevada, although there are many slight variations from the type as described above. Almost every valley exhibits forms not exactly like those in any other. The variations are chiefly in habit, pubescence, leafiness, size and shape of inflorescence, shape of bracts, and length of corolla-lobes. The plants range in height from a few dm. to nearly 3 m., but are always taller than broad unless abnormal; the corollas vary from 8 to 10 mm. in total length; the corolla-lobes are seldom shorter than 2 mm., yet in two collections there are some flowers with lobes only 1.7 mm. long; although the involucres of the type are only 6 to 7 mm. long, they vary in other specimens to 8 or even 9 mm.; the mature papus is 7 to 9 mm. long. A dwarf form of the alkali flats of Antelope Valley is referred here provisionally. It has flexuous stems, short rounded inflorescences and exceptionally small flowers (commonly 6 or 7 in a head), but the flowers, although reduced in size, have the narrow elongated and spreading lobes of *viridulus*. More nearly typical specimens have been gathered in the San Antonio Mountains at an altitude of 8000 feet, I. M. Johnston, no. 1706.

As to relationships, *viridulus* is probably a southwestern derivative of *consimilis* (or vice versa), from which it differs in the larger corollas with longer lobes, the thicker, more robust and rigid twigs and leaves, the heavier and more rounded inflorescence, and the stronger odor of the herbage. These characters are far from constant at all stations. The length of corolla-lobe is the most satisfactory. Of twenty-seven collections taken throughout the established range of the variety, only five have corolla-lobes 2 mm. or less long; of twenty-two collections from the range of *consimilis* none exhibit corolla-lobes of over 2 mm. in length; where the ranges meet as around Mono Lake and at Sodaville, Nevada, intermediate sizes are frequent and here the other differentiating characters also intergrade. The very long corolla-lobes serve as a certain means of distinguishing *viridulus* from all other varieties except *consimilis*, *occidentalis*, *bernardinus*, and an occasional *mohavensis*.

21. **Chrysothamnus nauseosus** var. **mohavensis** (Greene) comb. nov.

Bigelovia mohavensis Greene, *in* Gray, Syn. Fl., vol. 1, part 2, p. 138, 1884.
Chrysothamnus mohavensis Greene, Eryth., vol. 3, p. 113, 1895.

Shrub of medium or large size, with many erect or ascending branches which are often nearly leafless and rush-like: leaves filiform, very acute, 1-nerved, nearly glabrous: inflorescence a rounded or somewhat elongated thyrse: involucre narrow, 9 to 10 mm. long, sharply 5-angled; bracts obtuse to acute, in very distinct vertical ranks, glabrous: corolla 8 to 10 mm. long; lobes 1.5 to 1.8 mm. long, spreading.

In this variety we have apparently a southern derivative of *viridulus*. It belongs to higher ground where the drainage is better and the soil not obviously alkaline. It skirts the westerly side of Owens Valley, California, extending southward to the slopes west of Antelope Valley and swings around the latter as far as the desert slopes of the San Bernardino Mountains. It occurs also at an isolated station on Mt. Hamilton, far out of its general known range, but the specimens at that station seem entirely typical and Dr. Greene, the first to detect the form, himself admitted them as *mohavensis*. The species will probably be found elsewhere along the hot inner South Coast ranges, a little-explored district where many species of the southern deserts extend their ranges northward.

Although first described as sparsely leafy or leafless this character cannot be relied upon since the tendency toward an early dropping of the leaves is common to the whole group. It is true, however, that *mohavensis* is more commonly leafless or nearly so. The naked wand-like branches are sometimes much elongated, in one case measuring 7.5 dm. without leaf or branch (H. M. H., no. 10570). The best characters lie in the involucre, which is mostly longer than in the other forms. Although the longest involucres of *viridulus* slightly exceed the shortest ones of *mohavensis*, yet the average of the former is about 7 mm., of the latter about 9 mm. The bracts are distinctly five-ranked and carinate, so that the involucre is sharply five-angled. They are somewhat obtuse but in some specimens which are referable here by all other characters the bracts are decidedly acute (H. M. H., nos. 9894, 10570, 10611, and Hall and Babcock, no. 5090).

As indicative of the gradation between *mohavensis* and *viridulus* may be cited a specimen from Oak Creek, along the west side of Owens Valley (H. M. H., no. 10611). The habit is that of *mohavensis* although some of the twigs were leafy when gathered on October 30.

The tegules are in very sharply defined vertical ranks, as in that variety, but they are even more acute than in *viridulus;* and the corolla-lobes are exactly intermediate in length, measuring 2.1 mm.

22. **Chrysothamnus nauseosus** var. **junceus** (Greene) comb. nov.

Bigelovia juncea Greene, Bot. Gaz., vol. 6, p. 184, 1881.
Chrysothamnus junceus Greene, Eryth., vol. 3, p. 113, 1895.

Shrub strict, fastigiately much branched, with slender rush-like mostly leafless yellowish green branches: leaves linear-filiform: inflorescence fastigiate-cymose: involucre about 10 mm. high, glabrous; bracts acute, 5 in each of the distinct vertical rows: corolla about 9 mm. long; tube pubescent but not arachnoid; lobes about 1.5 mm. long, externally beset with long delicate hairs.

This is a little-known shrub of eastern Arizona. It is described by Greene as "cinereous"; by Gray as "minutely canescent", but the twigs in the type have the usual pannose tomentum and all other characters indicate that it belongs to the present group. The pubescence of the corolla-lobes should be distinctive if constant.

FORMS NOT DEFINITELY PLACED

The following named species are all very close to *Chrysothamnus nauseosus* and at least some of them should doubtless be included in that species when taken in its broadest sense. However, they are not sufficiently well known to the writer to justify him in passing upon them at present.

Chrysothamnus formosus Greene, Pitt., vol. 4, p. 41, 1899. A low white shrub with narrow spreading foliage and wholly glabrous involucres with 6 or 7 bracts in each vertical row. Described from immature plants gathered "in the neighborhood of a mineral spring among the hills a few miles southwest from Grand Junction, Colorado."

Chrysothamnus Macounii Greene, Pitt., vol. 5, p. 63, 1902. Said by Dr. Greene to resemble *plattensis* and like it a low plant with white-tomentose twigs and very narrow spreading leaves. The type was from near Lytton, British Columbia.

Chrysothamnus moquianus Greene, l.c., p. 60. Described from imperfect specimens but seemingly a variety of *nauseosus*, perhaps one of those with glabrous akenes.

Chrysothamnus turbinatus Rydb., Fl. Rocky Mts., p. 859, 1917 (*Bigelovia turbinata* M. E. Jones, Proc. Calif. Acad. Sci., ser. 2, vol. 5,

p. 691, 1895). Said to be next to *junceus* and with the uppermost leaves reduced as in that form but with glabrous corollas. The bracts are five or six in each row and all obtuse or only apiculate. The type locality is Canaan Ranch, Utah.

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II. CHRYSIL, A NEW RUBBER FROM *CHRYSOTHAMNUS NAUSEOSUS*

BY

HARVEY MONROE HALL AND THOMAS HARPER GOODSPEED

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I. OBJECT AND SCOPE OF THE INVESTIGATION[1]

The investigation here reported upon was instituted for the purpose of locating a supply of rubber which it was thought might exist in certain native West American shrubs. Of all the various species originally considered, those belonging to the genus *Chrysothamnus*, commonly known as Rabbit-brush, seemed to be the most promising, and consequently they have received the most attention.

This work was undertaken immediately after the entry of the United States into the recent war and had for its incentive a consideration of the following facts: that rubber is absolutely essential to modern warfare; that it is the only war essential not now produced in this country; and that, therefore, we as a warring nation would be seriously handicapped in case the enemy should be able to carry out his threats and put a stop to our oversea commerce. This danger of interference with our importation of rubber has now been happily averted but since no one is able to state with certainty that it may not recur, the location of a native supply is still a matter of national concern. Our studies have therefore been continued somewhat beyond the duration of the war and have resulted, as indicated in the following pages, in the finding of rubber of good quality in some of our western shrubs. If it were all assembled the total amount (estimated to be over 300,000,000 pounds) would be considerable, but the percentage content of the plants is too small to warrant harvesting except under stress of national emergency. The very fact that the shrub is not rich in rubber may have its advantages when the matter is viewed from the standpoint of the nation's needs. It means that the rubber will not be subjected to commercial exploitation and will thus be preserved as an emergency supply to be drawn upon only in case we reach such straits that its utilization becomes necessary notwithstanding the high cost of harvesting.

The very best protection against the possibility of enemy interference with our supply would be the development of a permanent rubber-producing industry in this country. Aside from the manufacture of synthetic rubber on a commercially profitable scale—a desideratum which does not seem to give promise of early realization—our only

[1] This investigation was carried out chiefly by members of the Department of Botany of the University of California and was one of the projects of the Subcommittee on Botany of the Committee on Scientific Research of the State Council of Defense of California.

hope for this lies in the discovery and improvement of plants which can be grown in this country and which will be sufficiently productive to warrant their cultivation in competition with imported rubbers. One such species has already been introduced—Mexican Guayule (*Parthenium argentatum*), now being grown to a limited extent in southern Arizona. There is no assurance, however, that this plant can be profitably grown over a sufficiently large area to supply the country's needs in time of war, nor are we certain that it is the best one to be used. It is desirable that all promising sorts should be carefully investigated and their possibilities determined. These reasons have led to a broadening of the scope of our inquiry to include a preliminary study of the cultural possibilities of the plants under consideration.

This extension of the scope of the investigation has emphasized our deficiencies in time and facilities for the satisfactory prosecution of the work. Since it has been carried on thus far as a purely war emergency matter, the aim has been to assemble our information as rapidly as possible, and we have not permitted ourselves to become unduly engrossed in any phase of the work that seemed to require a long period of study or experimentation. The authors regret this keenly, since it means that the report here presented must be very incomplete; that many fundamental questions regarding both the scientific and practical aspects of the subject must go unanswered. It seems our duty, however, to place on record such data as we have, including particularly such information as will assist those who may interest themselves in a further search for rubber-bearing plants. Methods of carrying out the histological examinations and chemical analyses are for the same reason given in detail though they may prove neither novel nor instructive to the trained botanist and chemist. It is hoped that this report will serve as a basis for more intensive researches, either by ourselves or by others, when conditions are more favorable and that it will point the way to special investigations that have to do with the formation and occurrence of rubber in these West American shrubs and its possible utilization by man.

The preliminary studies here described have been in progress for about two years but the work was carried on only during vacation periods and in such additional time as could be spared from regular university duties. In addition we have profited by the generous assistance of numerous co-workers to whom acknowledgment is made below.

The discovery of rubber in *Chrysothamnus*, which was made about fifteen years ago, has been described by us in a recent paper[2] as follows:

> The choice of *Chrysothamnus* and related genera as the plants first to be investigated was the result of a preliminary examination made in 1904. In September of that year the late Judge A. V. Davidson, of Independence, Inyo County, California, sent some twigs to the Department of Botany for identification, with the information that the Indians prepared from the plant a sort of "gum" which they chewed. The plant was a species of *Chrysothamnus* of the *graveolens* group. Further samples were submitted at our request, and in October, 1905, a preliminary chemical examination of them was made by Professor G. E. Colby, of the California Experiment Station. This examination indicated the presence of rubber, but not in sufficient amount to warrant further investigation. A report to this effect was made public in the press and as a result some further examinations were made by at least one commercial rubber company. The matter was soon dropped, however. It is probable that the plants used in this commercial examination were of an entirely different species from those now being examined.

The examination of 1904 was followed with field work by the senior author in Inyo County in 1906, but no further chemical examinations were made. Professor Marcus E. Jones informs us that steps were taken about 1908 to erect a rubber-extraction plant at Salida, Colorado, the intention being to use Rabbit-brush but the plan fell through. He also tells us that as early as 1878 the Indians near St. George, Utah, taught some Mormon boys how to prepare rubber by mastication of the inner bark of these plants. It is evident that the Indians have long made use of the rubber as a chewing gum, but we have been unable to learn of any scientific study of the plants as rubber producers up to the time of our preliminary work in 1904.[3]

II. ACKNOWLEDGMENTS

Throughout the course of the investigation the authors have had the valuable co-operation of a considerable number of workers, some of whom have given largely of their time without remuneration. In the early stages of the work the chemical analyses were made by Professor Paul L. Hibbard, in the laboratory of the Division of Agricultural Chemistry of the California Experiment Station and the staff of that laboratory, under the direction of Professor J. S. Burd, has given

[2] Science, n.s., vol. 47, p. 452 (May 10, 1918).

[3] Since the above was written word has come to us that a factory was in operation at Durango, Colorado, as early as 1905 and that the company in charge of it actually placed upon the market rubber made from "Rabbit-weed." However, the results of further inquiry indicate almost with certainty that the plant used was not *Chrysothamnus*, but the "Colorado Rubber Plant" (*Hymenoxys floribunda altilis*).

invaluable aid in the establishment and operation of our own laboratory, where the later analyses have been made by the junior author and Miss Mildred Crane. Dr. David Spence, Chairman of the Subcommittee on Rubber and Allied Substances of the National Research Council, has superintended the extraction and vulcanization of rubber from sample shrubs sent him and has given opinions from time to time regarding our methods and the quality of the product. Dr. W. B. McCallum, and Professor Francis E. Lloyd, both recognized experts on Guayule production, have made many valuable suggestions. Mr. E. C. McCarty of the University of California made a field trip of two weeks' duration into central Nevada for the purpose of collecting samples and making estimates as to the occurrence and distribution of certain species and Mr. J. R. Bruff, of the same institution, spent two weeks on such work in northern California and Nevada and southeastern Oregon. Professor Marcus E. Jones, of Salt Lake City, has performed a similar service in Utah. He spent a total of twenty days in the field and in addition has contributed freely from his very detailed knowledge of the botany and distribution of the shrubs throughout the Great Basin Area. Through the courtesy of Dr. Frederic E. Clements, of the Carnegie Institution of Washington, the senior author, was enabled to spend a month in field studies extending from Oregon to New Mexico. It is a pleasure to acknowledge also the assistance of Professor W. A. Setchell, head of the Department of Botany of the University of California, who has supported the work throughout both by his sympathy and advice and by making it possible for the authors to give to it a larger portion of their time than is ordinarily available for investigational work. The laboratories and herbarium of the Department of Botany have been freely used and much of the expense has been borne by the University. Grants have also been made, more especially for field expenses, by the Committee on Scientific Research of the State Council of Defense of California.

The list of friends who have sent information and samples, often at much trouble, includes the following: Mrs. Sidney Armer, Berkeley; Mr. W. W. Blakeslee, U. S. Forest Service; Mr. Fred E. Burlew, Los Angeles; Miss Ethel J. Case, Spokane; Mr. John Dondero, Mono Lake; Mrs. Roxana S. Ferris, Stanford University; Mr. M. French Gilman, Banning; Mr. Benj. J. Hoffner, U. S. Forest Service; Mr. Edmund C. Jaeger, Palm Springs; Mr. Geo. C. Larsen, U. S. Forest Service; Mr. W. M. Maule, U. S. Forest Service; Mr. James W. McGowan, U. S. Forest Service; Mr. Alexander McQueen, U. S. Forest

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To all of those who have assisted in the work, the authors tender their sincere thanks.

III. NATURE AND PROPERTIES OF CHRYSIL

Chrysil is the name here proposed for the rubber prepared from any form of *Chrysothamnus nauseosus*. It was suggested by Dr. Frederic E. Clements and is selected because of its euphony and brevity as well as for its suggestion of the botanical name of the plants from which the rubber is obtained. "Chrysothamnus" in turn, is derived from two Greek roots signifying "golden" and "wood."

The first samples of Chrysil were prepared for us by mastication from shrub of the *viridulus* form by Paiute Indians at Benton, California. These pieces were in the form of cylinders three-fourths to one inch long by about three-eighths of an inch in diameter. They included, in addition to the rubber, small amounts of resin, fiber, and other impurities. They were brown in color, firm, scarcely if at all tacky, and seemed to possess considerable strength and elasticity. Two experts accustomed to the handling of crude rubbers declared them to be "of good quality and considerably better than rubber prepared from Guayule." These samples were exposed to air and light and underwent a gradual change, so that at the end of a year they were black in color and quite tacky on the surface, these changes doubtless being due to impurities.

Twenty-five pounds of *viridulus* shrub were gathered from the flats at Benton and shipped to Dr. David Spence, Chairman of the Subcommittee on Rubber and Allied Substances of the National Research Council, with the request that he prepare rubber from it and

report on the yield and the quality of the product. The samples of shrub consisted of plants cut off a short distance below the surface of the soil and with all growth of less than three years removed; in other words, they consisted of those portions which would presumably be utilized in commercial operations. Dr. Spence very kindly undertook to make the examinations, and reports as follows regarding the preparation of the rubber and its properties:

In preparing the samples for analysis the woody ones were ground up on a pair of corrugated rolls, or a "cracker," and the bark samples were ground up and sheeted out on a smooth roll. It is interesting to note that the bark forms a smooth sheet on the mill.

.Each of the four samples was placed in a bottle, covered with 100% benzol and shaken one hour. It was then allowed to stand twelve hours and the liquor drained off. This washing was repeated twice. After allowing the small dirt to settle out, the three combined washes were distilled to a small bulk, 400 to 500 cc. The rubber was coagulated from this concentrated solution by the addition of pure methyl alcohol. The coagulated mass of rubber was kneaded in fresh methyl alcohol and vacuum dried at 95°C. The dried rubber is dark brown in color, has very little tackiness and considerable elasticity. When the solvents are removed by boiling in water, a very tacky rubber results.

A larger sample of bark from both stems and branches was extracted and the rubber obtained was compounded as follows: rubber 100 g., zinc oxide 100 g., accelerator 3 g., sulfur 6 g. This compound was then divided into five portions and these were vulcanized for thirty minutes, sixty minutes, ninety minutes, two hours, and three hours, respectively. Forty pounds of pressure was applied in each case. The sixty minute treatment under forty pounds was full cure.

These samples[4] indicate that the rubber vulcanizes readily and gives a product of a very fair quality. I have no hesitation in committing myself as to its value as far as it is possible to estimate this from such small samples as I was able to obtain. In order to report on the exact commercial value of this rubber it would be necessary to make many more tests and much more exhaustive ones, but from the small samples I sent you I can already safely say that the rubber is of high grade and average quality. It is not as good as the best fine Para, but it is a great deal better than most Africans or low grade rubbers. The results would indicate that the bark of shrub No. 64 (that is *viridulus*) might well be investigated more extensively as a possible source of crude rubber existent in this country.

IV. BOTANICAL CLASSIFICATION; THE NAMES OF THE PLANTS

The plants in which rubber has been found during the course of this investigation all belong to two closely related genera of the Compositae, namely *Chrysothamnus* and *Haplopappus*. The latter is apparently of little importance, for although rubber has now been

[4] The five samples referred to by Dr. Spence are in the form of circular discs one-fourth inch thick by one and one-fourth inches in diameter. They are preserved in the Botanical Museum of the University of California.

found in ten of its species and in rather large amounts in two of these, yet the high-percentage species are small plants. This genus will be dealt with elsewhere.[5]

The other, that is, *Chrysothamnus*, is a West American genus of about sixteen major species, but these include so many variations that some botanists would recognize more than one hundred specific segregates. Eleven of the major species of *Chrysothamnus* have now been examined and rubber found in five of them. One of these, *C. nauseosus*, is of outstanding promise; the other four are discussed further on.[6]

Botanists are far from agreement as to the limitation of species in the genus, but for practical purposes it seems best to adopt a broad species concept and to recognize a considerable number of varieties under each of the species. According to this arrangement *Chrysothamnus nauseosus* constitutes a major species with twenty-two varieties. Twelve of these have been examined for rubber and it was found to be present in all of them. The complete botanical designation of each variety may be expressed by a trinomial, for example, *Chrysothamnus nauseosus* var. *graveolens; Chrysothamnus nauseosus* var. *viridulus*, etc., but for simplicity we may be permitted, in a special paper such as the present one, to omit the generic and specific names and refer to the various forms only by their varietal names. We shall, therefore, use such detached terms as *graveolens* and *viridulus* to express our concept of the respective varieties belonging to the very complex species known as *Chrysothamnus nauseosus*. It is hoped that this simplification will appeal to the non-botanical reader, who often has little time for and less interest in an involved taxonomic terminology and that it will, at the same time, meet the needs of the professional botanist. In some cases the name of a species itself will be used independently of its generic name. The exact taxonomic position of any variety of *Chrysothamnus nauseosus* may be determined by reference to pages 159 to 181.

The correct common name of *Chrysothamnus*, and more particularly of *C. nauseosus*, and its varieties is Rabbit-brush, a name which has been in use both among non-botanists and in botanical literature for at least twenty-five years. Through erroneous identification it has been frequently applied to other plants. In two publications it has been used indiscriminately[7] for species of *Chrysothamnus*, *Tetradymia*,

[5] See pp. 268–274.

[6] See pp. 265–268.

[7] N. Am. Fauna, no. 35 (1913), pp. 28, 31, 37; no. 42 (1917), pp. 79, 81.

and *Gutierrezia* and in a recent Experiment Station bulletin it has been adopted for *Tetradymia glabrata*.[8] But on grounds of usage as well as priority the term "Rabbit-brush" should be used only for species of *Chrysothamnus*. It is defined in this sense in three of the leading dictionaries used in America and also in some designed more especially for use in Europe. "Rabbit-brush" is given as the common name for *Chrysothamnus* in at least fifteen floras and technical reports and, so far as we can discover, it has never been defined either in dictionaries or in floras as belonging to any other plant. While there is considerable misapplication of the term by stockmen and other residents of the West, yet it is much more frequently applied to these plants than to any others. The name "Golden Bush" is used somewhat in the Rocky Mountain states. The undiscriminating sometimes fail to distinguish between these plants and Sage-brush, but the true Sage-brush (*Artemisia tridentata*) is a very different plant and may be recognized by the leaves, which are, for the most part, three-toothed at the summit, whereas in the Rabbit-brush they are always entire.

The Paiute name for any sort of *Chrysothamnus* from which rubber is prepared is *tsigupi* (pronounced tsē-gōō-pēē); or if the plant grows in sandy soil it is called *teba-tsigupi*. It is possible that the older Indians restricted the use of *teba-tsigupi* to some particular variety, but the younger generation is not so discriminating. Dr. A. L. Kroeber, who has indicated for us the proper spelling of these words, says that *teba* means "sun." According to Dr. David P. Barrows, the Coahuilla Indians of southern California call the *graveolens* form *tes-i-nit* and prepare from its twigs a tea taken for coughs and pains in the chest.

V. *CHRYSOTHAMNUS NAUSEOSUS*: HABIT, FLOWERING, RATE OF GROWTH, ETC.

All of the species of *Chrysothamnus* are shrubs. Some are mere dwarfs but those which interest us as possible rubber producers are usually of good size, measuring three to eight feet high, and about as broad. The rubber is present for the most part in those stem parts which are three years old or more, and these portions in average mature plants of the more important varieties (*viridulus*, *hololeucus*, etc.) will weigh from five to fifteen pounds (2.3 to 6.8 kg.). An exceptionally large plant found near Lone Pine, California, weighed sixty pounds ex-

[8] Nevada Experiment Station, Bull. 95 (July, 1918), pp. 2, 7.

clusive of the twigs, and shrubs weighing twenty to forty pounds are not rare. For purposes of estimate, however, much smaller figures must be used. This is partly because the plants reach the maximum size only under favorable conditions and partly because they are frequently burned or cut off near the base, after which new stems shoot up only to be again destroyed before reaching maturity. After weighing numerous samples and after making thousands of estimates in the field the authors believe six pounds to be a fair average weight of the woody portions of the *viridulus* variety as it grows in eastern California and western Nevada. This includes the root to a depth of only four inches (10 cm.). This estimate does not include young seedlings nor young second growth.

On a similar basis it is estimated that individuals of *consimilis*, the common variety in northeastern California, Nevada, and western Utah, will average five pounds, while variety *pinifolius* of Utah, southern Colorado, etc., will average four or five pounds.

The rubber producing kinds of Rabbit-brush all grow from deep taproots which have normally but few main laterals. There are usually several trunks from a single base and these are clothed in age with loose, fibrous brown bark which peels off in strips. Straight clear stems are the exception. The branches are usually numerous; they often exhibit many distortions and irregularities and are of unequal size. This has a bearing upon the possibility of decortication by machinery, a point of considerable practical importance. The rubber is carried chiefly in the inner bark and in the very outermost portion of the wood, so that decortication would greatly reduce the bulk and weight of the material to be extracted. The irregularities just mentioned would presumably render decortication by machinery impracticable as far as wild shrub is concerned. If the plants are brought under cultivation they would be more regular and uniform in their growth and the separation of the outer layers might then become feasible. According to Dr. D. Spence the bark could be very easily separated from the wood on a large scale even in irregularly shaped plants by soaking in hot, dilute, caustic soda solution. The young shoots are long, straight, and erect in *viridulus;* similar but shorter in *graveolens* and *consimilis;* very much branched and twiggy in *gnaphalodes* and *hololeucus*. In all of these forms they are covered with a closely packed gray, green, or white felt-like tomentum which is deciduous only after several years. The narrow entire leaves are rather sparse and may be either green, as in *consimilis* and *graveolens*,

dull green as in *viridulus,* or gray as in *gnaphalodes.* In typical *nauseosus* and in *hololeucus* the foliage is entirely covered by a beautiful soft and white woolly tomentum.

The flowers are yellow, very showy, and grow in heads arranged in dome-shaped to oblong clusters terminating the stems. The plants are therefore highly ornamental during the flowering season, which extends from August to October. At that time the large round-topped shrubs are crowned with a profusion of golden-yellow flower-clusters. As winter advances the flowers wither and fall, the foliage becomes more and more sparse, and finally only the naked gray or dull green twigs and empty involucres remain. The young twigs then die back for a considerable distance. But soon after the first winter rains or snows new shoots, springing from lateral buds well down on the year-old wood, form a new top to the plant. Since the die-back of the annual shoots does not extend to the base the general height, or level, of the old wood is increased each year. At the same time there is a thickening of all of the older stems through the addition of another annual layer of wood. The flowers of *Chrysothamnus,* which are very small and assembled into heads, as in all the Compositae, are much visited by honey bees and other insects. This assures cross-pollination and there is no evidence that the flowers are self-fertile. Seeds are set in abundance, and they show a high percentage of viability. These characters enable the plants to occupy quickly any suitable area that has been cleared of other brush.

The herbage of *Chrysothamnus* possesses a peculiar odor which varies somewhat with the different forms. The name *nauseosus* indicates that the type of that species was disagreeably scented but this we have not been able to verify. In *viridulus,* however, the green stems when broken emit a very strong, disagreeable odor, especially penetrating if they are burned in a closed room. On the other hand, when the twigs and foliage of *gnaphalodes* and *hololeucus* are broken in the hand the odor is exceedingly pleasant, suggesting a combination of tropical fruits and berries. It seems probable that this is due to the presence of a volatile oil which might have commercial possibilities if properly exploited, more especially as a by-product in case the plants are brought under cultivation for their Chrysil.

The age of full-sized shrubs is quite variable, depending upon the conditions under which the shrubs have grown and also possibly upon the botanical variety concerned. An estimate based upon counts of annual rings, places the average age of the more important kinds,

such as *viridulus* and *consimilis*, at about eight years. This is for plants weighing five or six pounds and growing in ordinary alkaline soil without attention or disturbance by man. Plants seldom reach full size before they are five years old and they often increase in weight up to ten years and perhaps longer.

VI. DISTRIBUTION AND HABITATS OF THE VARIOUS FORMS

Rubber producing varieties of wild Rabbit-brush are widely distributed in western North America. They belong to the Lower and Upper Sonoran life zones with slight extensions into the Transition, and range in altitude from about sea level in some of the desert basins, to 8000 feet in the southern Colorado mountains. Some varieties of *Chrysothamnus* occur at even higher altitudes but they have not been examined as to their rubber content. The plants are most abundant and of maximum size in the Great Basin area, becoming more and more scattered and apparently diminishing in their percentage of rubber as we pass outward from this center of distribution. The northern limits are reached in British Columbia, Alberta, and Saskatchewan, but no detailed studies have been made of plants from those districts. They probably contain rubber in only limited quantity and the areas covered by the shrub are not extensive. Our northern tier of states supports some *Chrysothamnus* but only in the more arid portions such as southeastern Washington and southern Idaho and Montana. The most northerly points from which we have taken samples for analysis are in eastern Oregon (Redmond, Burns, etc.), eastern Washington (Spokane), southern Idaho, and southern Wyoming (Rawlins, Laramie). The best samples carried only 3 per cent of rubber and most of them ran less than two per cent. This low yield may be due to the habitat or it may be that a larger series of examinations would show that we happened to select only low-grade individuals and that the average is really as high as in districts lying farther to the south.

The easterly limits of the genus are reached in South Dakota and western Nebraska; the southerly limits in western Texas, southern New Mexico, and southern Arizona, with some possible extensions into Mexico, or at least into Lower California. Analyses have not been made of plants from these outlying districts but the indications are that they are not good rubber producers. On the Pacific Coast we find

scattered groups of the plants as far west as the Coast Range mountains, for example, San Benito County, Mt. Hamilton, Lake County, Trinity County, etc. Four samples of *mohavensis* from Mt. Hamilton averaged only 0.53 per cent of Chrysil.

Fig. 1. *Chrysothamnus nauseosus* var. *viridulus*. Plant no. 468. Seven feet high; growing in alkaline soil with *Distichlis spicata* and *Iva axillaris*. *Artemisia tridentata* in background. Goat Ranch, north of Mono Lake, California.

Coming now to the more important areas centering around the Great Basin, we find that some of the densest stands and also the largest plants are found in the alkaline deserts of Nevada and eastern California. There are some large and important areas of the brush in southern Colorado and in Utah, but the plants in these states are not as good rubber producers as those farther west. Throughout the whole

area Rabbit-brush is confined to certain definite tracts ranging in size from a few square feet to about 800,000 acres. It is prevented from growing in other places, sometimes by unfavorable soil, moisture, or climatic condition; sometimes by the more aggressive habits of other species with which it is obliged to compete. For example, when the soil is very strongly alkaline it is either devoid of vegetation or supports such strongly alkali-tolerant species as Grease-wood (*Sarcobatus*), Pickle-weed (*Salicornia*), Sea Blite (*Suaeda*), and *Spirostachys*.

Where the alkali is somewhat less in amount but still too abundant for upland plants certain varieties of Rabbit-brush, particularly the green forms such as *viridulus*, *graveolens*, and *consimilis* become dominant and with Salt-grass (*Distichlis*), Poverty-weed (*Iva axillaris*), and similar plants cover areas of considerable extent. Here are found the most extensive and important stands of rubber-producing shrub and the percentage of rubber is fairly high. The soil is somewhat moist but too strongly alkaline for standard agricultural crops and since the native grasses and other forage and browse plants are of but little use to stockmen the value of the land is very slight. The removal of the Rabbit-brush would favor the growth of grazing plants, as has been demonstrated by our experiments. However, the brush would again assert itself in a few years unless held in check. If it is found practicable to grow Rabbit-brush for its rubber, these extensive tracts could be had at a very low price and without serious interference to any established industry.

Passing upwards from the alkaline flats just described one often comes to better drained and scarcely alkaline slopes. Here the Sage-brush (*Artemisia tridentata*) is usually dominant and forms the extensive brush-lands of the Great Basin area. It mixes more or less with the Rabbit-brush varieties mentioned above, but it is less alkali-tolerant and so yields to them on the lowlands. On the slopes and higher plains and especially in loose soil, or along dry water-ways, the Sage-brush is often mixed with or replaced by another series of varieties of *Chrysothamnus*. These are the gray forms, particularly *nauseosus*, *speciosus*, *gnaphalodes*, *hololeucus*, and *frigidus*. The green and the gray forms intermingle slightly where they meet in soils of moderate alkalinity and moisture, but the latter are much more intimately associated with Sage-brush. In the terminology of the ecologist, the Sage-brush is climax, the gray Rabbit-brush is subclimax. In other words if the former is disturbed by fire, trampling, washout, etc., it is replaced by the Rabbit-brush, which, however, is in turn

slowly crowded out by a new generation of the more aggressive Sage-brush. The result is that the gray forms are much more scattered than the green ones and almost never form pure stands of any great extent. They are sufficiently abundant in some places to yield a supplementary supply of rubber in case the green forms are harvested from near-by areas, but they should not be considered in making estimates of the total amount of native rubber available. Their chief interest lies in the fact that they are very erratic as rubber producers and might therefore furnish starting points in case experiments were undertaken in the breeding or selection of superior strains.

VII. ESTIMATES BY DISTRICTS OF THE AMOUNT OF CHRYSIL AVAILABLE IN WESTERN NORTH AMERICA

Although field studies on the occurrence and distribution of rubber-bearing shrubs have been carried on in all of the western states, actual estimates have been made for only a few of the areas upon which they are known to grow. The sudden termination of the war has removed the immediate need of a complete survey, but if an emergency call is ever made the work thus far completed will furnish a starting point for a definite estimate of the total amount obtainable as well as indicate the localities where it may probably be found in the largest quantities. Somewhat detailed estimates for the areas examined are therefore presented by districts.

This phase of the work has been carried on chiefly by the senior author, who has himself visited a majority of the areas reported upon and who assumes full responsibility for the estimates here given. His studies have been supplemented by those of a number of other botanists as mentioned on page 186.

The estimates were prepared in the following manner. Districts where the brush grows abundantly were visited and traversed when possible in several directions. Data thus accumulated, supplemented by such information as could be obtained from reliable residents, furnished rough estimates of the acreage covered, the percentage of vacant land within the area, and the ratio of Rabbit-brush to other shrubs. Small quadrats were then selected and the number of plants per acre determined. Average samples were weighed or at least estimated as to weight. From these data the total tonnage of shrub has been calculated. A sufficient number of samples has been analyzed

from widely separated geographic areas, and of the many botanical varieties to furnish something of a basis for the calculation of the total amount of rubber present on any given area, the total tonnage having been determined in the manner just described. While these results are far from satisfactory because of the meager data upon which they are based they will furnish at least a beginning in case more extensive investigations are inaugurated, and will indicate the best locations for rubber mills in case the government is ever obliged to resort to Rabbit-brush as a source of rubber in time of emergency.

The areas indicated in the following list include, we believe, most of those where Rabbit-brush is abundant, yet it is quite certain that at least a few large areas have escaped our hasty field survey. It is well known that, in addition, there is a multitude of small fields of the shrub and also that it often grows scatteringly where other species are dominant. However, because of the great expense of assembling shrub from small scattered fields, this source is not included in the estimates.

a. DISTRICT 1—EAST CENTRAL CALIFORNIA AND ADJACENT NEVADA

This district comprises Inyo and Mono counties in California, and an extension into Esmeralda County, Nevada, chiefly to include Fish Lake Valley. In it are found large areas of shrub carrying over 3 per cent of rubber, although the total area of shrub is much smaller than in some of the other districts where the percentage content is less. The chief variety included in the estimate is *viridulus*, which is larger, on the average, than any of the others. It occurs chiefly on the alkaline valley bottoms but ranges sparingly to altitudes of 7200 feet in alkaline soil. Mixing somewhat with it around the borders of the valleys, where the soil is better drained and less alkaline, are considerable quantites of *gnaphalodes*, *hololeucus*, and *mohavensis*. These extend well up the foothill slopes but always as mixtures in the Sage-brush climax—never as pure stands. North and east of Mono Lake, *viridulus* is replaced to some extent by *consimilis*. There is also a supplementary supply, furnished by the very considerable amount of *Chrysothamnus teretifolius*, a low shrub carrying about 2.7 per cent rubber; but since the plants are somewhat scattered it does not enter into our estimates (see p. 266).

Some of the best shrub in this district is found in Owens Valley, where it grows on most of the flats along the river; in an irregular strip along the Los Angeles aqueduct; and on isolated areas of from

one-half to several square miles in extent. Some of the largest plants seen anywhere grow near the aqueduct (but not irrigated from it) a few miles north of Lone Pine. The district around Keeler has not been examined, nor has Long Valley, although both are reported to have some Rabbit-brush. A considerable area in the lower part of Deep Spring Valley is also said to be covered with Rabbit-brush of the

Fig. 2. *Chrysothamnus nauseosus* var. *viridulus*, mingling with var. *graphalodes*. Experimental tract, Lone Pine, California. Soil moderately alkaline, much trampled. Sierra Nevada Mountains in background; Mount Whitney at right of center.

viridulus variety. If harvested, probably the best place to take it for milling would be Owens Valley. Small lots are also obtainable to the northeast of Owens Valley, particularly in the vicinity of Benton, whence come our richest samples of *viridulus*, and in Chidago Cañon, etc. Our estimate of the total amount of rubber in Owens Valley and contiguous territory is 300,000 pounds.

Fish Lake Valley, in western Esmeralda County, Nevada, is included in District 1 since the size, habit, and variety of the shrub is similar to that around Mono Lake and in Owens Valley. The exact botanical classification of the plants, however, is not satisfactory. They

grow in varying degrees of density over most of the valley bottom except where farming operations have interferred. An estimate based upon a hurried visit in 1918 and upon data supplied by Forest Ranger George Parke places the total amount of rubber at 2,280,000 pounds.

Extensive areas of Rabbit-brush have been located in the vicinity of Mono Lake, but our analyses indicate that it is not so rich as that from Owens Valley and Benton. The principal varieties represented are *viridulus* and *consimilis*. There are about ten square miles of fairly large plants to the north and northeast of the lake in a nearly pure stand. On the south and southwest sides it is mixed with Sage-brush over an area of perhaps sixteen square miles. In Adobe Valley, which lies southeast of the lake, we find it in good formation from the Adobe Hills to the River Spring Ranch and in a narrower belt as far as Dutch Pete's while there are perhaps a thousand acres of it in a belt extending from Gaspipe to Indian Spring. By using the methods indicated above, we have estimated that these areas centering around Mono Lake would yield about 700,000 pounds of rubber.

The estimated total amount of rubber obtainable from District 1 is 3,280,000 pounds.

b. DISTRICT 2—MOJAVE DESERT, CALIFORNIA

This might almost as well be called the "Antelope Valley District" since it centers around this westerly arm of the Mojave Desert. It is not very promising as a rubber producer because of the large number of varieties represented and the consequent fluctuation in rubber content. The largest continuous area of shrub is a belt of *gnaphalodes* about two miles wide and perhaps thirty miles long, which extends diagonally across the valley in a northwesterly direction from near Palmdale to a point west of Rosamond. The shrubs are below medium size, the woody portion weighing on the average about three pounds, and there are about 50,000 plants per square mile. A similar belt is reported still farther west. These belts are undoubtedly due in large part to the burning off or clearing of the Sage-brush in the remote past and represent one stage in the succession which will ultimately bring this Sage-brush back as the dominant climax species. Analyses indicate that this shrub carries an average of two per cent of rubber. Smaller areas of *gnaphalodes* are scattered all around the borders of Antelope Valley and even to Tehachapi Pass and northward to Owens Lake, mixing slightly along its upper limits with *mohavensis*, but the lower, more alkaline lands support a scattered growth of what ap-

pears to be a dwarf form of *viridulus*. Most of these small plants carry less than two or three per cent of rubber and are of but little practical importance.

C. teretifolius, carrying about 2.7 per cent of rubber, grows sparsely on the Rosamond Hills but may be abundant on the mountains to the west of Antelope Valley. Around the borders of the Mojave Desert, especially toward the west, are scattered stands of two other low-grade rubber shrubs, *Haplopappus monactis* and *H. linearifolius,* but these are of little value.

The amount of rubber in the shrub which we have located in District 2, taking no account of the species mentioned in the preceding paragraph, is estimated at 400,000 pounds.

c. DISTRICT 3—NORTHEASTERN CALIFORNIA AND ADJACENT NEVADA AND OREGON

The principal areas thus far located in this district are on the alkaline plains of eastern Lassen and Modoc counties, California, where Rabbit-brush, in the *consimilis* form, makes pure stands over many thousands of acres. The percentage of rubber in these plants is apparently quite uniform and runs a little more than two per cent. There are about two square miles east of Honey Lake where the plants average sixteen feet apart and two representative samples weighed ten and twenty-eight pounds, respectively. In the vicinity of Karlo we find about seven square miles covered by a nearly pure stand of the shrub; an area of about the same size occurs on Painter's Flat; and still another to the west of Madeline. The plants on these tracts are often smaller than in the Honey Lake Valley (two taken near Karlo weighed under two pounds each for the woody portion), but when small they grow closer together. There is an area of 1000 acres south from Ravendale, covered with medium sized shrub. About twenty square miles have been located by Mr. L. S. Smith in northeastern Modoc County, where the Rabbit-brush comprises about 25 per cent of the vegetation, but it occurs chiefly in one of the gray-foliaged varieties and is therefore poor in rubber. There are some unexamined areas of *consimilis* west of Alturas, several sections of the gray form in Butte Valley and around Klamath Lake, and some extensive areas of *consimilis* on the Klamath River drainage of north-central Siskiyou County, California.

In southeastern Oregon, the Rabbit-brush was found by Mr. J. R. Bruff to exist only in small stands. The largest area located is in

Blitzen Valley, where there are perhaps twelve square miles of *consimilis*, and in Catlow Valley, where there is a somewhat smaller area of the same form. Studies made by the senior author from Burns to Bend and northward indicate that the plants there grow too sparsely to be of interest and that the percentage content is not uniform. Reports of large areas at Buffalo Meadows and on the Black Rock Desert of Nevada were found to be erroneous and it seems that there is but little of the shrub in the northwestern corner of that state. It is interesting to note, however, that two samples of the variety *consimilis* gathered along the edges of the alkali flats near Gerlach yielded the highest returns of all of the samples taken of *Chrysothamnus nauseosus*. They analyzed 4.71 and 6.57 per cent, respectively, of pure rubber.

The most important areas in this district are to be found, therefore in eastern Lassen County, California, and in Blitzen and Catlow valleys of southern Oregon. The total amount of rubber in the shrubs thus far located in District 3 is estimated at about 1,000,000 pounds.

d. DISTRICT 4—WEST CENTRAL NEVADA

This small district lies wholly in Nevada and is between the California boundary and a line connecting Hazen and Tonopah. On the north it is limited by the line of the Southern Pacific Railway; on the south, by an east-and-west line passing through Tonopah.

The only variety of *Chrysothamnus* to be considered here as a possible source of rubber is *consimilis*, but this grows in abundance in valley bottoms where the soil is somewhat sandy, slightly moist, and, for the most part, too alkaline for Sage-brush. Around the edges of such areas, and running back into the hills, it is not uncommon to find other varieties, especially those of the gray types like *griseus*, *nauseosus*, and *speciosus*, but these occur as impurities in the Sage-brush consociation and are therefore too scattered to be of consequence as a possible source of rubber.

The *consimilis* form varies much in size and habit, depending in these characters upon soil and climatic conditions. Exceptionally large plants were encountered on the flats at the head of Walker Lake. These were six feet high and almost tree-like, with trunks five inches thick and over a foot in length to the first main branches. Such plants have a weight of about thirty pounds, exclusive of twigs. The average weight of samples, however, taken from along Walker River, north of the lake is about ten pounds, while the average for the whole dis-

trict is nearer six pounds. The rubber content of seven samples taken at widely separated stations in the district averages 2.0 per cent and microscopic examinations of others indicate that there is not a wide fluctuation from this mean.

Fig. 3. *Chrysothamnus nauseosus* var. *consimilis*. Plant no. 216, Walker Lake, Nevada. Root two and three-eighths inches thick; trunk five inches thick at base of first branch; total height six feet; estimated weight about thirty pounds. This is an exceptionally large plant.

The southernmost areas of Rabbit-brush within this district are in Esmeralda County and lie along the Tonopah and Goldfield Railroad from Redlich nearly to Millers, one of them extending as a belt along the westerly side of the San Antonio Wash. Small areas of large brush were found at the upper end of Walker Lake, but much more import-

ant is the irregular belt which skirts the river on both sides from a point about nine miles above Schurz nearly to Wabuska, a distance of eighteen miles. This belt will average three-eighths of a mile in width; the plants are ten to twelve feet apart and have an average weight of about ten pounds. Forest Supervisor W. M. Maule reports about fifty square miles of shrub from Whiskey Flat north to Hawthorne; also about thirty-five square miles between Sweetwater and Fletchers. These areas are in western Mineral County. We have not ourselves visited them and have not had an opportunity to examine samples.

The Carson Valley and contiguous areas support about one-hundred and fifty square miles of Rabbit-brush of the *consimilis* form. Several other forms are present, some of them apparently devoid of rubber, but they grow scatteringly around the borders of the main bodies and extend up over the slopes as impurities in the sage-brush. It is on the lower, more nearly level, and alkaline flats of the valley that the best stands of *consimilis* are found. Here it often grows to the exclusion of other shrubs, and almost completely covers the ground with plants weighing three to five pounds.

According to our estimates, District 4 should yield at least 7,680,000 pounds of rubber, of which nearly one-half is in or near the Carson Valley. It is probable that further exploration would result in a considerable addition to this estimate.

c. DISTRICT 5—NORTHERN AND CENTRAL NEVADA

By E. C. McCarty

This district comprises the counties of Humboldt, Leander, Eureka, Elko, White Pine, and a part of Nye County. In view of the many areas in this section which are favorable to the growth of *Chrysothamnus*, it would without doubt prove to be an important one in the production of an emergency supply of raw rubber. The long valley of the Humboldt River, extending through the counties of Elko, Eureka, Leander, and Humbolt, has many tributary valleys extending both to the north and to the south, and ranging from comparatively short valleys to valleys of more than fifty miles, the Reese River Valley being one of the longer ones.

The Reese River Valley, which is perhaps typical, is half a mile wide at Cañon, and more than fifteen miles wide at Austin. It extends the entire length of Leander County and into Nye County. The mountain range is continuous on either side of the valley and is marked at

frequent intervals by draws and gulches from which flow the streams tributary to the Reese River. This river has an interrupted flow through the greater part of the valley though it is itself a very small stream. The floor of the valley is comparatively level, and rises gradually to the mountains on either side. The altitude, which is four thousand five hundred feet at Battle Mountain, increases at the southerly end to upward of six thousand feet. The soil is alkaline and is of the type usually found in arid regions. The precipitation is meager; the greater portion probably occurs in the fall and winter. The summers are comparatively long and the number of days of sunshine in one year probably approaches three hundred. The coldest temperature experienced by the writer while in this valley during the month of December, 1918, was —15° F.

The character of both soil and climate permits the growth of only drought-resistant vegetation. Generally speaking, the lowest lands of the valley floor are occupied by *Chrysothamnus*, while the more elevated portions are covered for the most part with *Artemisia*. Much of the lowlands is covered with pure stands of *Chrysothamnus*. Again large tracts occur in which this shrub represents fifty per cent of the entire stand. Along the river bottom the dominant shrub is *Chrysothamnus,* but in many places in the immediate vicinity of the stream the soil appears to be fairly moist in character, and is occupied by willows. In such sections, which are comparatively few, *Chrysothamnus* occupies the zone next to the willows and on either side of the stream. At many places in the valley the brush, in stands more or less pure, extends into the draws and gulches. Where the *Chrysothamnus* forms occur to the practical exclusion of other types, the stands are quite dense, the plants averaging from four to ten feet apart. It is believed that the pure stands occupy those parts of the valley in which the physiological drought of the soil reaches the maximum.

The pure stands of *Chrysothamnus* throughout the entire district are for the most part of the *consimilis* form. While there are some comparatively small areas of the gray varieties, these seldom occur in pure stands, and none of this type are included in the estimate for the district. The size of the green brush is variable. Some of the plants are quite large, the height being three to eight feet. While some of the larger ones would weigh as much as twenty-five pounds, it is not difficult to find others that would weigh still more. The average, however, is much lower, and the weights employed for the purpose of the estimates in this report are between two and seven

pounds. These figures, however, are based on the weight of a small portion of the root, and of the stems upwards of four years of age. Should it become desirable to use the younger wood the average weight would be increased by one to two pounds. It is probable that the amount of brush now available will remain constant for a number of years, since the character of the soil and climate is more favorable to stock raising[9] than to agriculture.

While many of the points in this district have been visited and are known to contain large tracts of *Chrysothamnus*, reliable information has been received in other ways relative to the occurrence of large stands in those sections which were not visited. The character of this information and the source whence it has come warrant the inclusion of these several areas in the estimate of available brush in the district. On the other hand the combined areas reported on and included in the estimate are but a part of the entire territory comprising the district. In view of the similarity in topography, in climate, and in soil conditions prevailing throughout this entire region it is believed that a more intensive survey of the district might reveal still other tracts of the shrub which in the aggregate would equal those included in this report.

The principal areas thus far located are the following:

Elko County: Ten Mile Flat; North Fork, Humboldt River Valley and tributary valleys; along the main line, Southern Pacific and Western Pacific railroads; Ruby Valley; along the Nevada Northern Railroad, Cobre to Goshute.

Eureka County: Along the main line, Southern Pacific and Western Pacific railroads; Antelope Valley.

Humboldt County: Areas lying 6 and 15 miles, respectively, northeast of Winnemucca; Rebel Creek; Quinn River Valley.

Leander and Nye counties: Along the main line of Southern Pacific and Western Pacific railroads; Reese River Valley; Big Smoky Valley (north end); Monitor Valley; Fish Spring.

White Pine County: Butte Valley; Long Valley; Newark Valley; Spring Valley; Steptoe Valley; White River Valley.

The total weight of Rabbit-brush known to exist in this district has been placed at 1,250,000,000 pounds. Twenty-three samples have been gathered and analyzed. The rubber content of these samples varies from 0.43 to 3.86 per cent, with an average of 1.89 per cent. On the basis of these figures the total available supply thus far located

[9] It is reported that *Chrysothamnus* is poisonous to range stock during the winter season.

would be 23,700,000 pounds of pure rubber. It must be borne in mind that these estimates are based on the weight of plants after the removal of the foliage and of all stems under four years of age.

f. DISTRICT 6—UTAH

Within the state of Utah, Rabbit-brush in several forms occurs over extensive areas, especially around the alkaline valleys of the central and southeasterly parts of the state. Much information as to the location of shrub in quantity has been assembled by Professor Marcus E. Jones, but an examination of the samples supplied by him indicates that the rubber content is less than that of plants from Nevada and California. The analyses we have made of his plants average only 1.12 per cent for the *consimilis* variety, which is by far the most abundant one, but this is perhaps too low an average for all of the Utah shrub, since three samples of *consimilis* collected by ourselves near Stockton carried 1.31, 2.46, and 2.84 per cent of rubber, respectively. Whatever the exact average may be, it certainly is low and renders unnecessary the publication of detailed information as to distribution. The largest areas of shrub in Utah lie along the alkaline flats of Sevier Valley, Tooele Valley (and south to beyond Vernon), Tintic Valley, Rush Valley, Utah Valley, Juab Valley, and the valleys of the Price and Green rivers. By far the largest stand of shrub is along the Sevier River, where Professor Jones finds a strip about one-fourth mile wide by one hundred and fifteen miles long, extending from Panguitch north to Fayette, and he describes other large areas in that valley. In the valleys of northeastern Utah, such as the Uinta Basin, *Chrysothamnus* occurs only in small, isolated patches and is of no importance in preparing estimates. In northwestern Utah, the varieties present are those which carry but little if any rubber and there are no extensive areas even of these. To the southwest, however, there are some stands of *consimilis* that should be taken into account. There is one area of at least 20,000 acres along the line of the Salt Lake Railroad and farther south than any of those mentioned above. The shrubs are closely placed but quite small, the average weight being estimated at scarcely over one pound. A sample taken at Milford yielded 1.24 per cent of rubber. A single sample of *C. turbinatus* gathered on the plains near Lund analyzed 4.88 per cent of rubber. This species is too scarce to be of importance save as a starting point in breeding experiments.

According to Professor Jones, the average weight of Utah plants, after cutting off the twigs, is about fifteen pounds, but in order to be perfectly safe we have taken only ten pounds as the weight in making up our estimates.

From the data indicated above and taking 1.12 per cent as the average content, we estimate the total amount of rubber present in *Chrysothamnus* in Utah to be not less than 20,000,000 pounds.

g. DISTRICT 7—COLORADO

Our explorations in this state have been far from exhaustive, consisting only of one visit to the northwestern part, a north-and-south journey along the easterly base of the Rocky Mountains, a visit to the San Luis Valley, and notes and samples taken along the line of the Denver & Rio Grande Railroad. The only important area of *Chrysothamnus* that we have located is in the San Luis Valley of south central Colorado, where we estimate, from observation and from reports of reliable residents, that not less than 800,000 acres are fairly well covered with *Chrysothamnus* of the *pinifolius* variety. Over much of this area the plants stand about ten feet apart, that is, there are about four hundred and thirty-five plants to the acre. Since Grease-wood, or Chico (*Sarcobatus vermiculatus*) and other impurities occur in some portions of the valley, we have taken only one-half of this number as a basis for estimates. The plants are of medium size, the average weight after the removal of the non-rubber-bearing portions being perhaps five pounds. Two samples taken at Alamosa yielded 3.41 per cent and 1.11 per cent, respectively. A third, sent from near Center by Mr. Wm. O. Sauder, analyzed 3.59 per cent. This makes an average of 2.70 per cent of pure rubber. On this basis the total amount of rubber present in this one valley would be about 24,300,000 pounds. This is probably the largest single body of shrub in Colorado, if not in the whole West. Smaller but otherwise similar areas doubtless occur in some of the unvisited river valleys of the southwestern part of the state.[10] Along the Gunnison we found only small detached areas of Rabbit-brush and the same is true of the valley of the Yampa, in northwestern Colorado.

The most easterly stations at which we have found rubber-bearing shrubs lie along the east base of the Rocky Mountains from Fort Collins and Denver to Trinidad. Five samples of *graveolens* from these

[10] See p. 186, footnote.

places averaged less than 1 per cent of rubber and nowhere did we find other than small groups of the plants. A single sample of *frigidus* from Laramie, Wyoming, was found to carry 1.86 per cent of rubber. A sample of *pinifolius* from Salida yielded 4 per cent.

Our estimate of the total amount of rubber present in *Chrysothamnus* in Colorado is based entirely upon what was found in the San Luis Valley and is therefore, as indicated above, about 24,300,000 pounds.

h. ESTIMATES NOT INCLUDED IN THE ABOVE DISTRICTS

There are many districts in addition to those just enumerated that will need to be explored before a final statement as to the occurrence of rubber-bearing shrubs can be made. Large bodies of these plants might be found in any of the western states. The most promising of these, in addition to those already specifically mentioned, is perhaps Wyoming. It is well known that this state supports large areas of Rabbit-brush but aside from a few samples taken along the southern border we have made no study of its rubber possibilities. We have been told also of considerable areas in southern Montana, in Idaho, and in eastern Washington, but judging from the varieties there present the percentage of rubber in the plants is very low. In Nevada, which we have covered as well as any other state, there are still some promising unexplored fields. *Chrysothamnus* occurs in a number of species and varieties in New Mexico, according to good authority,[11] but we have scarcely considered that state. Professor A. O. Weese reports a great deal in the region around Albuquerque. Arizona is likewise a state of possibilities, but the areas of Rabbit-brush to be found there are probably quite limited in extent. These two southerly states should be carefully explored in case a search is made for new strains of high quality, since a considerable number of species and variants not yet examined are known to occur and the climatic conditions are such as would be expected to result in the formation of rubber.

i. CONCLUSIONS AS TO THE QUANTITY OF RUBBER OBTAINABLE

As previously noted, the explorations in search of rubber plants have not extended to all parts of the West, nor, indeed, has any single

[11] Vernon Bailey, Life Zones and Crop Zones of New Mexico. N. Am. Fauna, no. 35 (1913), pp. 28, 31, 37.
Wooton and Standley, Flora of New Mexico. Contrib. U. S. Nat. Herb., vol. 19 (1915), pp. 660–663.

state been thoroughly examined. The seven districts reported upon, however, furnish some indication of the total amount of rubber that might be obtained in case of need. The estimated amount already located by districts is as follows:

	Pounds
District 1—East Central California and adjacent Nevada	3,280,000
District 2—Mojave Desert, California	400,000
District 3—Northeastern California and adjacent Nevada and Oregon	1,000,000
District 4—West Central Nevada	7,680,000
District 5—Northern and Central Nevada	23,700,000
District 6—Utah	20,000,000
District 7—Colorado	24,300,000
	80,360,000

Taking this total of approximately 80,000,000 pounds as representing the probable amount of pure rubber present in the shrub located, it is believed that this estimate could be safely increased by 50 per cent by allowing for the presence of other areas within these districts, although we have not been able to visit them. After this has been done, we have still to account for several whole states as well as several fractions of states lying outside the seven districts noted above. We hesitate to venture a guess as to what these might yield but it seems probable that the total amount in all of the western states is not less than 300,000,000 pounds.

VIII. METHODS OF DETECTING THE PRESENCE OF RUBBER AND DETERMINING ITS AMOUNT

a. MICROSCOPICAL METHODS

Microscopical examinations of *Chrysothamnus* and related genera were at first undertaken as a short cut method of determining whether or not a given sample of shrub contained rubber. In addition we have attempted, with some success, to employ the microscopical method for estimating the relative amounts of rubber in the different samples. At the beginning of the investigations we were forced to rely upon this method almost entirely since facilities could not be secured for making ourselves the many chemical analyses which have since been carried through. Chemical analysis is, of course, the only method of making both the original determination and of obtaining an estimate of rubber present which is at once thoroughly dependable and really significant.

The microscopical method, in brief, consists in the cutting of cross sections of a mature portion of the sample and the making therefrom, after the action of suitable solvents, stains and mounting media, of a preparation in which the rubber, if present, may be seen under the microscope. As will be shown in the detailed description given below, the process of making such a preparation is simple and may be sufficiently well controlled to yield results that will be fairly uniform and reliable.

As in Guayule, the rubber in *Chrysothamnus* and *Haplopappus* is present within the individual cells of the plant, and is not a latex rubber. Like Guayule again it is found principally in the parenchymatous elements of the cortex; indeed it may occur in any undifferentiated elements lying without the cambium or, in other words, in what is often spoken of as the "soft" or "inner bark." It may also be noted here that rubber does not appear to be laid down during the first year of growth of a tissue and indeed, unless present in large amount, is not readily detected by the histological method in portions of the plant less than three or four years old. A section of a plant taken slightly above the soil line will exhibit tissues containing practically maximum quantities of rubber. In investigating new and untried species by the microscopical method it is wise to make sections from well down the root as well as at the soil line. This is indicated by our results on *Haplopappus* mentioned in the third part of this report. In certain species of that genus practically no rubber was found in sections of stem tissue, while quite appreciable amounts were shown in sections taken well down the main root. We have found in *Chrysothamnus* that maximum quantities are borne by the stem, although for a limited distance below the soil line the root may bear an almost equivalent amount.

In selecting and removing the material to be sectioned care must be exercised to retain the bark. This is often difficult, as the dry corky tissues readily split off, together with the living cortex, along the delicate cambium region, from the hard, woody cylinder. When the tissues are stripped off in this way it is useless to attempt the cutting of sections, since practically the entire rubber-bearing cortical area will be missing. It has been our practice to cut out the desired piece of mature woody tissue[12] and allow it to soak in water for twenty-four hours before sectioning. This treatment softens all the tissues and

[12] We have found that a coping saw can be very successfully employed to cut out the piece of stem to be sectioned.

renders more simple the handling of the important barky elements. The actual cross sections are made with a section knife or heavy-backed razor not hollow ground. The piece of material may be held in the fingers for cutting or in a so-called hand or well microtome. One of us has devised a modification of this type of microtome which was used in these investigations.[13] A sliding microtome has also been used. Successful sections can be cut only with an extremely sharp instrument and only a few sections can be cut before sharpening must be repeated. Smoothing the surface to be cut with a sharp pocket knife is desirable and saves for a time the finer edge of the sectioning razor. If interest centers entirely upon the question of the presence or absence of rubber, it is not essential that the sections cut be particularly thin nor that they be taken exactly at right angles to the long axis of the sample. In our work details of structure and other matters were often of special importance for which reason all sections were cut less than 50μ in thickness and were carefully oriented.

As noted by Lloyd[14] rubber when present in large amount is, after some practice, rather readily detected in fresh or unstained sections of non-latex rubber plants. When present in smaller quantities it is often indistinguishable from the protoplasmic matrix of the cell or is confused with accumulations of oil or resin in the tissues. According to our histological method oils and resins were dissolved out because of the relatively small amount of rubber usually present and especially as a preliminary to the use of a stain which was not definitive for rubber in the presence of these other substances. As a solvent, acetone was used exclusively, the sections being placed in a test tube half full of acetone and allowed to stand in a water bath at 60° C. for from fifteen to thirty minutes. For staining the sections we at first tried alkanin,[15] but Sudan III was early found to be more satisfactory and was therefore employed in the great majority of the histological examinations. Our Sudan III was made up with glycerine according to Stevens' formula.[16] This stain imparts a brilliant scarlet color to fats, resins and rubbers as they occur in the cell. By the previous acetone extraction fats and resins had been dissolved from the cell contents but rubber was left practically unaffected and if present took up the stain. The stain was allowed to act for eighteen hours, after which the

[13] Goodspeed, T. H., Modification of hand microtome. Bot. Gaz., vol. 66 (1918), p. 534.

[14] Lloyd, F. E., Guayule. Carnegie Inst. Publ. no. 139 (1911), p. 176.

[15] Cf. Stevens, W. C., Plant anatomy, 3d ed. (1916), p. 293.

[16] *L.c.*, p. 337.

excess was washed from the sections with 50 per cent alcohol. The sections were then mounted in glycerine and in some cases were ringed.

Some search has been made for a staining method which would be strictly definitive for rubber and which would result in imparting such a characteristic color to the rubber cell-inclusions as would serve to distinguish them definitely from all other inclusions. The desirability of securing such a staining method is seen in the fact noted above, that alkanin and Sudan III are in histological practice used to indicate the presence of resins and fats, respectively, and thus their ability to stain rubber in the cell is in a sense more or less fortuitous. The fact that alkalin is a specific stain for resins might suggest a corresponding staining reaction in the case of rubber. As far as Sudan III is concerned, however, we are employing a stain used in animal histology to give definition to globules of fat occurring in the cell. Without going into the question of the chemistry and differential staining of the fats, fatty acids, and lipoids, it may be noted that the staining of fat globules by Sudan III is taken to indicate that this stain is soluble in the contents of the fat globule whereas it is not soluble in the other constituents of the cell which, therefore, remain unstained. It is somewhat difficult with this explanation of the characteristic staining reaction of Sudan III in mind, to understand its action in the case of rubber. This matter is mentioned simply to call attention to the possible theoretical interest attached to the problem of the staining of rubber inclusions in the cell.

We have, further, been interested in this matter because cell inclusions have been consistently found in chlorophyllous tissue of both stems and leaves which, with Sudan III, stained as rubber, but which were difficult to differentiate with this stain from the residue of the protoplast with its included chloroplasts, which does not in such tissue entirely disappear after acetone extraction and which stains to some extent with Sudan III. In this connection it should be stated that in other tissues also it is difficult to distinguish between the protoplasmic matrices of the cells which may be stained with Sudan III and the rubber inclusions which may or may not be present. Thus in the tables which follow it is in some cases possible that the plants which on the basis of "microscopical examination" are stated to contain "traces" of rubber may have shown only stained cell inclusions which could not positively be identified as rubber.

We have made some preliminary investigation of the effects of a variety of stains. A number of staining combinations were attempted,

especially in the case of sections involving chlorophyllous tissue, to stain the protoplasmic matrix of the cell and follow with Sudan III. It appears that a heavy staining with Orange G. followed by Sudan III may be a useful combination in this connection. Of a number of stains ordinarily employed for the differentiation of the elements of woody tissue one at least gave some indication of being of interest. Sections were placed in Delafield's haematoxylin for twelve hours, partially destained and placed over night in Sudan III. In the resulting preparation the rubber inclusions were stained scarlet by Sudan III while in the center of each was a single spot of dark purple indicating, apparently, that each rubber globule contains a protoplasmic "nucleus" around which it is built up. Results of this sort indicate a field for further investigation.

It occurred to us, also, that vulcanization of the rubber *in situ* might be possible, and thus giving specific differentiation under the microscope to rubber inclusions in the cell. After suitable dehydration, sections were placed in the cold in sulfur chloride (in carbon tetracholoride) or were allowed to stand in the fumes of such a solution. The results of a number of preliminary experiments indicated that vulcanization of the rubber inclusions in the cells was possible.

The following outline of the process of making preparations of rubber-containing tissue described in some detail above may be of assistance to those who may desire to make histological examinations for a similar purpose. Attention must be called to the fact that nothing original is claimed for this process, nor will it necessarily prove successful in all its details for other species.

It is assumed that a woody plant is under investigation and that sections have been cut from a sample of mature tissue.

(1) Sections from water to 95 per cent alcohol; 5 minutes.

(2) Boiling acetone; 15 to 30 minutes.

(3) Sudan III; 18 hours.

(4) Wash off excess of stain in 50 per cent alcohol; as rapidly as possible.

(5) Mount in pure glycerine.

A preparation made in this manner from material cut from a relatively high percentage plant of *Chrysothamnus nauseosus* will show cell inclusions of rubber stained a brilliant scarlet. At a magnification of 150 diameters the parenchymatous elements of the cortex and especially the broad wedge-shaped cortical extensions of the primary

rays will appear to be solidly filled with stainable material. In the younger corky layers of the inner bark stainable cell inclusions will probably be numerous. Nearer the periphery a tissue which is often intensely stained will usually be found, with greater magnification, to consist largely of much crushed bark cells the suberized walls of which take up the stain readily. Within the cell the rubber occurs in globular form or in a more or less diffused state filling the entire cell cavity. The globules may be large, one or two to a cell, or small and numerous in each cell (cf. plate 18, figs. 4 and 5). Only this brief description will be made here of the appearance of a typical preparation made according to the process detailed above. The subject of the occurrence of rubber in the plant and in the cell is treated of in some detail elsewhere (cf. p. 234).

As mentioned in an earlier paragraph, we have attempted with some success to use the microscopical method for estimating the relative amounts of rubber in the various samples examined. A purely arbitrary scale of values was adopted and relative rubber content determined in each case by comparison with other preparations selected as representing high, low, and medium rubber content. For such comparisons a comparison-ocular was found to be useful. Uniformity in the quality and quantity of the illumination is quite important and artificial light was therefore used throughout. As soon as it became possible to obtain large numbers of chemical analyses the histological method of estimation became largely superfluous. However, in almost all cases it was resorted to prior to the chemical analysis and a rough estimate made. Often when the rubber content of a sample appeared to be quite low no chemical analysis was made, and a considerable amount of time and labor was thus saved. Throughout the investigation we continued to examine microscopically numbers of samples of doubtfully valuable species which were suspected by others of containing rubber or which were collected by ourselves in order that no possible source of rubber accessible to us should be overlooked.

We have found the microscopical method invaluable in many phases of this investigation. The question as to the place and time of the origin of rubber in the plant can only be answered by employing this method. Furthermore, supplemented by chemical analysis it gives important evidence concerning the parts of the plant which carry rubber and their richness relative to age and location. Ultimately the season and method of harvesting such a rubber crop will be determined largely on the basis of information so derived.

b. CHEMICAL ANALYSIS

The original chemical analysis of *Chrysothamnus* was made in October, 1905, by Professor G. E. Colby of the California Experiment Station. At the start of our investigations in 1917 a few analyses were very kindly made for us by Professor P. L. Hibbard of the same station. The great majority of the analyses listed in the various tables which follow were made under the direction of the junior author, in whose laboratory the necessary grinding and extraction apparatus was set up.

The particular method of chemical analysis which we have almost exclusively employed consists in the thorough extraction of a finely ground sample of material, first with acetone and second with benzene. The acetone extract is taken to contain approximately all resins, fats, and similar bodies; the benzene extract to contain the rubber. A detailed schedule of the whole process is given below for the convenience and assistance of those who may care to make use of this method or some improvement upon it. It is to be understood that the periods of extraction as well as the length of the periods of drying to constant weight were definitely determined after a large number of preliminary efforts. The few early extractions were made with one of the numerous modifications of the Soxhlet apparatus, while for the great majority the Bailey-Walker extractor was employed. The acetone extraction was made over the water-bath, the benzene extraction on electric hot plates. The method may be summarized as follows:

(1) Five-gram sample extracted 3 hours, boiling acetone.

(2) Acetone flask dried 8 hours, cooled in desiccator and weighed.

(3) Material in extraction thimble or siphon tube dried, placed in a second flask, and subjected to action of boiling benzene for 3 hours.

(4) Flask containing benzene extract dried 4 hours, cooled in desiccator, and weighed.

Two layers of filter paper were placed at the bottom of the siphon tube, as well as a plug of cotton. So complete a protection was this arrangement against the coming over of particles of the sample that filtration of the solution at the completion of the extraction was not necessary. Similarly, a plug of cotton placed upon the top of the material in the siphon tube obviated any danger of an overflowing of

the finely divided sample, especially as the bottom of the condenser pressed down on this cotton plug during the course of the extraction.

In almost all cases the first of the acetone-soluble substances extracted were strongly colored and turned the solvent a dark greenish brown as soon as the extraction commenced. Thereafter the liquid passing through the siphon tube was practically colorless. The benzene extract was in practically all cases entirely without color. The acetone extract after drying was very dark brown in color and strongly odorous. The benzene extract when dry was on the other hand colored light brown or yellowish, was almost entirely odorless, and was distinctly rubber-like in consistency.

There are, of course, a variety of other methods of analysis which might possibly have successfully replaced the one which we have employed throughout. For the sake of comparison we made trial of another method, according to which the sample is first extracted thoroughly with gasoline, then treated with strong sodium hydroxide, then filtered, and the residue, finally, extracted with carbon tetrachloride. This method is far more time-consuming than the one which we have used and appeared to offer no real advantages as compared with it. In the extraction of Guayule shrub on a large scale gasoline is sometimes used as the solvent and acetone as a precipitant. The recovery of these reagents used in large quantity in such a process is a complicated problem but it can be accomplished with very slight losses. Moisture determinations were made in most cases.

The following table indicates something as to the relative accuracy of our chemical analyses. Duplicate or triplicate analyses were often run in cases where comparisons were to be made with analyses of other parts of the same plant or with equivalent portions of a given individual collected on various different dates. The figures given are selected as being representative. They indicate a relative degree of accuracy for our analyses, sufficient at least to give an estimate of the average amount of rubber contained in the various species with which we have been concerned.

Table 1.—The Results of a Number of Duplicate Analyses

	Species or variety	Place of Collection	Date of Collection 1918	Acetone Extract Per cent.	Benzene Extract Per cent.
157	Haplopappus ericoides	San Francisco, Calif.	July 27	6.67	2.10
		San Francisco, Calif.	July 27	4.99	1.89
203	C. n. gnaphalodes*	Kearsarge, Inyo Co., Calif.	Jan. 28	2.81	1.45
		Kearsarge, Inyo Co., Calif.	Jan. 28	2.56	1.46
206	Haplopappus nanus	Near Benton, Calif.	Feb. 19	9.57	6.72
		Near Benton, Calif.	Feb. 19	10.41	6.88
220	C. n. consimilis	Near Wabuska, Nev.	Feb. 27	3.69	2.75
		Near Wabuska, Nev.	Feb. 27	3.62	2.95
240	C. n. speciosus	Near Weed, Calif.	June 6	2.90	1.48
		Near Weed, Calif.	June 6	2.43	1.52
255	C. n. speciosus	East of Hammett, Idaho	June 22	4.59	2.67
		East of Hammett, Idaho	June 22	4.65	2.56
		East of Hammett, Idaho	June 22	5.19	2.49
		East of Hammett, Idaho	June 22	4.69	2.70
		East of Hammett, Idaho	June 22	4.16	2.52
		East of Hammett, Idaho	June 22	4.06	2.60
		East of Hammett, Idaho	June 22	4.20	2.58
257	C. n. consimilis	Shoshone Falls, Idaho	June 23	3.90	2.63
		Shoshone Falls, Idaho	June 23	3.51	2.56
290	C. n. pinifolius	Alamosa, Colo.	Aug. 31	4.27	3.41
		Alamosa, Colo.	Aug. 31	4.70	3.40
		Alamosa, Colo.	Aug. 31	4.23	3.59

In this and following tables the initial letters C. n. are used to indicate *Chrysothamnus nauseosus.*

The reduction by maceration and grinding of woody plants for detailed chemical analysis of the contents of their tissues is at best attended with some difficulty. The difficulties were somewhat magnified in the material with which we worked, since the wood of most species of *Chrysothamnus* is quite hard and since, also, it was necessary in most cases to grind green shrub.

Each plant to be analyzed was trimmed with care. Since it seemed clear that for all practical purposes the older portions of the main stem contained maximum quantities of rubber, all the younger shoots and most of the root was eliminated previous to grinding. Figure 4 shows portions of a representative plant of *Chrysothamnus nauseosus* var. *viridulus* trimmed in this way and ready for grinding.

Usually such large plants were cut up into a number of equivalent portions, alternate pieces being used for grinding. In some cases where the plants were unusually large the trimmed mass was split longitudinally into portions as nearly equivalent as possible. In this connection may be mentioned the difficulty of performing this operation successfully. It is evident that the including of "bark" belonging

Fig. 4. Portions of a representative plant of *Chrysothamnus nauseosus* var. *viridulus* trimmed and ready for grinding.

to one portion along with the portion to be ground will decidedly affect the rubber content of the ground sample since the greater part of the rubber is contained in the extra-cambial elements of the stem. To test this matter we ran a few analyses of ground material from both portions of a number of plants. The results are given in the following table.

TABLE 2.—VARIATION IN RUBBER CONTENT DUE TO UNEQUAL SEPARATION, SHOWN BY ANALYSES OF BOTH HALVES OF LARGE PLANTS WHICH HAD BEEN SPLIT LONGITUDINALLY

	Species	Place of Collection	Date of Collection 1918	Acetone Extract Per cent.	Benzene Extract Per cent.
455	C. n. consimilis	Adobe Valley, Calif.	Sept. 19	3.70	2.55
		Adobe Valley, Calif.	Sept. 19	3.75	2.44*
		Adobe Valley, Calif.	Sept. 19	3.21	2.81
457	C. n. consimilis	Gaspipe, Calif.	Sept. 19	3.66	1.95
		Gaspipe, Calif.	Sept. 19	2.97	2.07
467	C. n. viridulus	North of Mono Lake, Calif.	Sept. 22	3.71	1.74
		North of Mono Lake, Calif.	Sept. 22	2.28	2.47

* Duplicate analysis.

These figures indicate that care must be exercised in splitting off portions of a plant for grinding and analysis. As noted above it has been almost uniformly our practice to cut up larger plants into transverse sections and grind alternate pieces.

For the first rough crushing or grinding a small power driven feed mill proved satisfactory. The material was run through this mill a number of times, the grinding plates being continually brought nearer together until the maximum degree of fineness was attained. At this stage practically all the material could be passed through a 10-mesh sieve. For the final grinding a hand-operated No. 0 Enterprise coffee mill proved successful. The final result of this last grinding was the production of material that would pass through a 24-mesh sieve.

We have attempted with some success to substitute the action of a pebble mill for the greater part of the final grinding.[17] Since the rubber is held within the walls of the individual cells and since, even when put into solution by benzene, these confining walls must serve to hinder outward diffusion of the rubber to some extent, it seemed

[17] A modification of a small Abbe pebble mill ("single specimen mill") was used. Mention might here be made of the fact that there are on the market a number of power driven grinding machines which would undoubtedly perform an initial reduction to 10-mesh much more rapidly and evenly than the apparatus described above.

clear that previous to extraction the finest possible subdivision of the plant material was desirable. Preliminary tests indicated that after prolonged grinding in the pebble mill a greater reduction in size of particles was attained than by our usual final grinding in the coffee mill. Examination of the pebbles at the end of their action showed particles of rubber as well as woody and fibrous tissue adhering to their surfaces. We therefore made a number of analyses to determine, if possible, just what proportion of the rubber was left behind on the pebbles after pebble mill grinding. The following table indicates the relation in each case between the amount of rubber extracted from a sample of the ground material as it came out of the pebble mill and the amount extracted from another portion of the same rough ground material which had been reduced in the coffee mill. Attention should be called to the fact that no rubber was found to adhere to the metal grinding plates of the feed mill or coffee mill and that both were taken apart and brushed out after each grinding, the material remaining in the mills being added to the ground substance which had gone through them. In a few cases material was ground in a pebble mill operated in the Food and Drug Laboratory of the University of California. This mill was larger than ours and the product was somewhat more finely divided than the product of our pebble mill.

Table 3.—Influence Upon the Results of Analysis of Final Grinding in a Coffee Mill and in a Pebble Mill

	Species	Acetone Extract Per cent.	Benzene Extract Per cent.	Remarks
87	C. n. gnaphalodes	2.78	0.59	Coffee mill.
		3.07	0.46	Pebble mill. 4 hours.
133	C. n. viridulus	4.12	3.64	Coffee mill.
		4.60	4.06	Pebble mill. 4 hours.
134	C. n. viridulus	3.73	2.18	Coffee mill.
		3.93	2.14	Pebble mill. 4 hours.
135	C. n. viridulus	4.57	1.30	Coffee mill.
		3.69	1.29	Pebble mill. 6 hours.
		4.07	1.22	Pebble mill (Food & Drug Lab.)
140	C. n. consimilis	4.76	3.86	Coffee mill.
		5.50	3.89	Pebble mill. 4 hours.
144	C. n. consimilis	3.75	0.81	Coffee mill.
		3.74	0.79	Pebble mill. 4 hours.
146	C. n. consimilis	3.69	1.74	Coffee mill.
		3.54	1.54	Pebble mill. 4 hours.

Table 3.—(Continued)

	Species	Acetone Extract Per cent.	Benzene Extract Per cent.	Remarks
149	Haplopappus ericoides	9.17	3.92	Coffee mill.
		7.88	2.48	Pebble mill. 4 hours.
		7.47	3.11	Coffee mill.
		5.53	2.50	Pebble mill. 4 hours.
215	C. n. gnaphalodes	4.29	2.57	Coffee mill.
		4.29	1.92	Pebble mill. 4 hours.
227	C. n. consimilis	3.98	2.14	Coffee mill.
		4.30	2.12	Pebble mill. 4 hours.
229	C. n. speciosus	3.55	2.49	Coffee mill.
		4.83	2.37	Pebble mill. 6 hours.
		4.72	2.07	Pebble mill (Food & Drug Lab.)

Although, as in all such cases, a far larger number of analyses is necessary to give entirely reliable evidence it appears from the figures given above that the product of the pebble mill, irrespective of the fact that some rubber is kept behind on the pebbles, yields approximately as large an amount of rubber as does the product of the coffee mill. The results given in the following table leave no room for doubt that rubber does adhere to the pebbles.

Table 4.—Evidence that Rubber Adheres to the Pebbles when Material is Ground in a Pebble Mill

	Species	Acetone Extract Per cent.	Benzene Extract Per cent.	Remarks
206	Haplopappus nanus	9.57	6.72	Coffee mill.
		8.71	6.22	Pebble mill. 4 hours.
		8.88	8.51	Pebble mill. 4 hours. Pebbles washed in benzene and solution filtered. Residue (2gm.) added to ground material (3gm.) and whole extracted with filtrate.

In view of these results the conclusion seems inevitable that the degree of fineness of the ground material is an important factor in the extraction of rubber from non-latex rubber-bearing plants according to our method of chemical analysis. Apparently the added fineness of the product of the pebble mill facilitates the thorough extraction of the rubber to such an extent that the amount of rubber added by this more nearly complete extraction compensates for the amount retained upon the pebbles. In other words if over 2 per cent of rubber is held on the pebbles, as is indicated by the results given in table 4, one might expect that the benzene extract from pebble mill material would be approximately 2 per cent less than that from coffee

mill material. In fact, however, these two analyses were in most cases approximately the same and this result is assumed to depend upon the fact that the finer division of the product of the pebble mill allows the extraction of 2 per cent more rubber than was possible in the case of the coarser product of the coffee mill.

With these facts in mind we decided to make the final grinding of all our samples in the coffee mill since the matter of removing the rubber adhering to the pebbles of the pebble mill is somewhat difficult and time-consuming. This was done as a matter of practicability notwithstanding the knowledge that the results would be too low to express the actual percentages present. The discrepancy, however, cannot be anywhere near the 2 per cent mentioned since that referred to a plant in which the rubber content is much higher than the average, and one moreover in which the very resinous material adhered to the pebbles more persistently than in most cases. It is believed that the amount of rubber remaining in samples of *Chrysothamnus nauseosus* after grinding in a coffee mill and extracting by our method seldom if ever approaches 1 per cent of the original sample.

In a preliminary way, at least, we have obtained evidence as to the effect of storage of the ground material upon rubber content. At the start of our investigations it was assumed that if for any reason a plant was not analyzed almost immediately after collection a deterioration in content and quality of the contained rubber would soon render the result of its analysis of doubtful value. Undoubtedly the exposure of shrub to drying and weathering out of doors will bring about such deterioration in the course of time (cf. Lloyd, *l.c.*, p. 10). As has been noted above (p. 220) it is difficult so to divide a plant for analysis that the halves or apparently equivalent portions will give closely corresponding analyses. For this reason we did not attempt, in seeking evidence as to the influence of storage upon rubber content, to analyze a portion of a plant and after subsequent storage for some months analyze an apparently equivalent portion represented by the remainder of the same plant. Rather the residue, after the first analysis, of the ground material of a plant was stored in a stoppered bottle and analyzed after a time. We have assumed that the amount of deterioration in such a finely ground sample after storage approximates that which might be expected to occur within the tissues of an entire plant after a corresponding period of time. The table which follows details the results of a number of analyses of ground material shortly after the original dates of collection and after periods of storage varying from five to ten months.

TABLE 5.—EFFECT OF STORAGE OF GROUND MATERIAL UPON RESULTS OF CHEMICAL ANALYSES

Collection Number	Species	Place of Collection	Date of Collection	Date of Analysis	Acetone Extract Per cent.	Benzene Extract Per cent.	Remarks
206	Haplopappus nanus	Near Benton, Calif.	Feb. 19, 1918	June 18, 1918	9.57	6.72	Stem
				Jan. 25, 1919	8.37	6.61	Stem, after 6 months
				June 18, 1918	5.96	5.29	Root
				June 18, 1918	6.02	6.40	Root, dup. analysis
				Jan. 25, 1919	6.53	6.42	Root, after 6 months
				Jan. 25, 1919	6.46	6.53	Root, dup. analysis
240	C. n. speciosus	Near Weed, Oregon	June 6, 1918	June 28, 1918	3.06	1.50	Stem
				April 5, 1919	2.90	1.48	Stem, after 10 months
				April 5, 1919	2.43	1.52	Stem, dup. analysis
255	C. n. speciosus	East of Hammett, Idaho	June 22, 1918	July 15, 1918	4.59	2.67	Stem
				July 15, 1918	4.65	2.56	Stem, dup. analysis
				July 15, 1918	5.19	2.49	Stem, another dup. an'is
				July 28, 1918	4.69	2.70	Stem, another dup. an'is
				Jan. 26, 1919	4.16	2.52	Stem, after 6 months
				Jan. 26, 1919	4.06	2.60	Stem, dup. analysis
				Jan. 26, 1919	4.20	2.58	Stem, another dup. an'is
256	Haplopappus nanus	Shoshone Falls, Idaho	June 23, 1918	July 10, 1918	5.86	4.61	Stem
				July 18, 1918	5.90	4.66	Stem, dup. analysis
				Jan. 26, 1919	4.94	4.54	Stem, after 6 months
				Jan. 26, 1919	5.33	4.46	Stem, dup. analysis
257	C. n. consimilis	Shoshone Falls, Idaho	June 23, 1918	July 22, 1918	4.32	2.70	Stem
				April 5, 1919	3.90	2.63	Stem, after 9 months
				April 5, 1919	3.51	2.56	Stem, dup. analysis
279	C. n. graveolens	Trinidad, Colo.	Aug. 11, 1918	Sept. 8, 1918	2.65	1.03	Stem
				Sept. 8, 1918	2.44	0.94	Stem, dup. analysis
				April 14, 1919	2.44	0.91	Stem, after 7 months
				April 14, 1919	2.16	0.93	Stem, dup. analysis
416	Haplopappus nanus	Caliente, Nev.	Sept. 6, 1918	Sept. 24, 1918	4.49	8.42	Stem
				Jan. 25, 1919	3.59	8.23	Stem, after 5 months
				Jan. 25, 1919	4.12	8.41	Stem, dup. analysis

It seems clear from the above figures that there is little to be feared in the way of loss of rubber by the storage for some months of the ground material of such rubber bearing plants as those which we have investigated. It is assumed that a similar statement can be made for plants in their original condition when stored in the laboratory or mill under more or less uniform conditions of temperature and moisture.

Attention might be called to the fact that in table 5 it appears that the content of acetone-soluble substances in general shows a somewhat greater diminution in amount following storage than does the rubber content. Further experiments along this general line are planned since evidence may, seemingly, be obtained regarding the relation between resins as well as other acetone soluble substances and rubber. Indeed other analyses of stored material, not so well controlled and therefore not included in table 5, indicate that accompanying the loss of resins, etc., there is an actual increase in rubber after storage.

It had been our original intention to include in the various tables which follow the date of analysis as well as the date of collection. Since the period elapsing between these two dates seems to have little or no influence upon the rubber content of a plant the former date was eliminated. It should be said, however, that every effort was made to analyze the various plants as soon as possible after they were brought into the laboratory. In the majority of cases less than a month or six weeks intervened between collection and analysis.

IX. RESULTS OF THE CHEMICAL ANALYSES AND MICROSCOPICAL EXAMINATIONS; TABULATION OF PERCENTAGE OF RUBBER IN EACH VARIETY

The methods employed in making the chemical analyses and microscopical examinations have been detailed elsewhere (cf. p. 210). The following tables give the results of such analyses and examinations as were made on individual plants of a number of varieties of *C. nauseosus*. As in previous tables the collection number is included for the sake of completeness and for future reference. The date of analysis is not given because of considerations mentioned above. The "X" following certain of the percentages indicates that they are not based upon dry weight. In all other cases moisture determinations were made, and the figures are based upon dry weight.

The terms used in describing the amount of rubber determined by microscopical examination are only relative and are derived from a more elaborate classification used during the course of the investigations.

In the reports on the chemical analyses, the first column, or "acetone extract" is taken to represent the percentage of resins, fats, waxes, etc., in the sample while the second column indicates the percentage of pure rubber, or Chrysil. As indicated on page 223, the figures in this second column are probably too low by a fraction of 1 per cent in each case owing to the difficulty of obtaining the proper degree of fineness in grinding the samples.

A summary of these tables is given on page 244.

We are under great obligation to Miss Mildred Crane who undertook the carrying through of the majority of the chemical analyses and assisted during the entire investigation in a variety of ways.

TABLE 6.—RESULTS OF CHEMICAL ANALYSES AND MICROSCOPICAL EXAMINATIONS OF INDIVIDUAL PLANTS OF TWELVE VARIETIES OF *Chrysothamnus nauseosus*

Chrysothamnus nauseosus (*sensu strictu*)

MICROSCOPICAL EXAMINATIONS

	Place of Collection	Date of Collection	Estimated Amount
251	Near Harney, Ore.	June 19, 1918	Nothing
463	Mono Lake, Calif.	Sept. 20, 1918	Traces

Chrysothamnus nauseosus var. **consimilis**

Chemical Analyses

	Place of Collection	Date of Collection	Acetone Extract Per cent.	Benzene Extract Per cent.
16	Deeth, Nev.	June 17, 1917	3.10	2.30
139	Golconda, Nev.	Mar. 4, 1918	4.72	2.21
140	Golconda, Nev.	Mar. 4, 1918	4.76	3.86
141	Golconda, Nev.	Mar. 4, 1918	5.12	3.71
142	Golconda, Nev.	Mar. 4, 1918	4.70	2.27
143	Golconda, Nev.	Mar. 4, 1918	3.85	1.07
144	Golconda, Nev.	Mar. 4, 1918	3.75	0.81
145	Golconda, Nev.	Mar. 4, 1918	3.59	2.12
146	Golconda, Nev.	Mar. 4, 1918	3.69	1.74
208	Near Blair Junction, Nev.	Feb. 24, 1918	5.58	2.90
210	Near Millers, Nev.	Feb. 24, 1918	3.67	4.17
214	Schurz, Nev.	Feb. 26, 1918	4.32	0.99
216	Schurz, Nev.	Feb. 26, 1918	3.62	0.65
217	Walker River, Nev.	Feb. 27, 1918	4.77	1.27
218	Walker River, Nev.	Feb. 27, 1918	3.79	2.17
219	Walker River, Nev.	Feb. 27, 1918	5.06	1.03
220	Near Wabuska, Nev.	Feb. 27, 1918	3.69	2.75
227	Karlo, Modoc Co., Calif.	Mar. 7, 1918	3.98	2.14
231	Karlo, Modoc Co., Calif.	Mar. 8, 1918	4.26	2.23
232	Honey Lake Valley, Calif.	Mar. 9, 1918	5.17	2.43
241	Near Weed, Calif.	June 6, 1918	3.25	1.02
250	Near Burns, Ore.	June 19, 1918	2.55	0.89
253	Near Ontario, Ore.	June 20, 1918	3.57	3.14
254	Southeast of Mt. Horne, Idaho	June 20, 1918	2.50	0.46[x]
257	Shoshone Falls, Idaho	June 23, 1918	3.90	2.63
402	Stockton Lake, Utah	Sept. 3, 1918	2.28	2.46
403	Stockton Lake, Utah	Sept. 3, 1918	3.14	1.31
404	Stockton, Utah	Sept. 3, 1918	3.91	2.84
408	Milford, Utah	Sept. 4, 1918	4.64	1.25
430	Goldfield, Nev.	Sept. 9, 1918	1.65	1.69
455	Adobe Valley, Calif.	Sept. 19, 1918	3.70	2.55
456	Adobe Valley, Calif.	Sept. 19, 1918	4.77	2.84
457	Gaspipe, Calif.	Sept. 19, 1918	3.66	1.95
472	Near Mountain House, Nev.	Sept. 22, 1918	3.44	1.26
473	Carson, Nev.	Sept. 23, 1918	2.08	2.85
474	Carson, Nev.	Sept. 23, 1918	2.70	2.30
475	North side of Carson River, Nev.	Sept. 23, 1918	4.62	2.42
476	South side of Carson River, Nev.	Sept. 23, 1918	3.14	0.59
477	Southeast of Gardnerville, Nev.	Sept. 23, 1918	3.75	0.83
478	South of Carson, Nev.	Sept. 23, 1918	2.82	3.54
479	East of Carson, Nev.	Sept. 23, 1918	3.12	3.79
480	Near Dayton, Nev.	Sept. 23, 1918	3.92	1.97
507	Stockton Lake, Utah	Sept. 25, 1918	1.74	0.20
514	Cedar Valley, Utah	Oct. 12, 1918	2.43	0.15
519	Muskrat Springs, Utah	Oct. 24, 1918	2.73	0.48
520	Near Josepha, Utah	Oct. 24, 1918	3.16	1.23
522	Tooele Valley, Utah	Oct. 24, 1918	3.47	0.62
523	Vernon, Utah	Oct. 24, 1918	2.64	0.67[x]
524	Utah Lake, Utah	Oct. 30, 1918	2.69	1.63
527	Sanpete Valley, Utah	Nov. 12, 1918	3.00	1.25[x]

Chemical Analyses (Continued)

	Place of Collection	Date of Collection	Acetone Extract Per cent.	Benzene Extract Per cent.
527a	Sanpete Valley, Utah	Nov. 12, 1918	2.46	0.39[N]
528	Redmond, Utah	Nov. 12, 1918	3.10	3.48[N]
528a	Redmond, Utah	Nov. 12, 1918	2.33	1.77[N]
530	Circle City, Utah	Nov. 12, 1918	3.04	1.26[N]
532	Panguitch, Utah	Nov. 12, 1918	2.90	2.00[N]
533	Mona, Utah	Nov. 12, 1918	2.52	0.82[N]
534	Goshen, Utah	Nov. 18, 1918	2.80	0.81[N]
600	Golconda, Nev.	Dec. 23, 1918	3.30	1.51
602	Watts, Nev.	Dec. 24, 1918	3.27	1.58
603	Reese River Valley, Nev.	Dec. 25, 1918	3.72	1.07
604	Battle Mountain, Nev.	Dec. 28, 1918	3.41	2.98
605	Near Ely, Nev.	Dec. 30, 1918	2.98	0.54
606	Near Ely, Nev.	Dec. 30, 1918	3.64	1.84
607	Near McGill, Nev.	Dec. 31, 1918	3.80	1.15
608	Near McGill, Nev.	Dec. 31, 1918	3.04	1.04
609	Shafter, Nev.	Jan. 1, 1919	5.06	3.04
610	Shafter, Nev.	Jan. 1, 1919	4.15	1.21
611	Lamoille, Nev.	Jan. 2, 1919	3.13	1.08
613	Near Elko, Nev.	Jan. 2, 1919	3.66	0.43
614	North fork of Humboldt River, Nev.	Jan. 3, 1919	3.42	1.07
615	North fork of Humboldt River, Nev.	Jan. 3, 1919	3.36	0.93
650	Near Macdoel, Siskiyou Co., Calif.	Dec. 25, 1918	3.35	1.57
651	Blitzen Valley, Ore.	Dec. 27, 1918	2.91	0.78
652	Catlow Valley, Ore.	Dec. 29, 1918	3.44	2.06
653	Warner Valley, Ore.	Dec. 29, 1918	4.00	1.68
654	Warner Valley, Ore.	Dec. 29, 1918	3.25	0.84
655	Warner Valley, Ore.	Dec. 29, 1918	2.95	1.43
656	Quinn River Valley, Nev.	Jan. 3, 1919	4.79	3.36
657	Quinn River Valley, Nev.	Jan. 3, 1919	3.64	2.83
659	Near Gerlach, Nev.	Jan. 3, 1919	4.23	4.71
660	Near Gerlach, Nev.	Jan. 3, 1919	3.08	6.57

Microscopical Examinations

	Place of Collection	Date of Collection	Estimated Amount
11	Pyramid Lake Road, Nev.	June 14, 1917	Fair
26	Goldfield, Nev.	Aug. 10, 1917	Fair
32	Pyramid Lake Road, Nev.	Aug. 16, 1917	Fair
159	Near Magdalena, New Mex.	July 22, 1918	Poor
233	Honey Lake Valley, Calif.	Mar. 9, 1918	Fair
252	Near Westfall, Ore.	June 20, 1918	Traces
258	Southeast of Burley, Idaho	June 24, 1918	Traces
260	Southeast of Albion, Idaho	June 24, 1918	Traces
261	Southeast of Snowville, Utah	June 25, 1918	Poor
263	Near Duchesne, Utah	June 30, 1918	Traces
417	Caliente, Nev.	Sept. 6, 1918	Traces
502	Grantsville, Utah	Sept. 25, 1918	Traces
505	Stockton Lake, Utah	Sept. 25, 1918	Nothing
506	Stockton Lake, Utah	Sept. 25, 1918	Traces
513	Cedar Valley, Utah	Oct. 12, 1918	Poor
521	Near Josepha, Utah	Oct. 24, 1918	Poor
525	Near Jericho, Utah	Oct. 30, 1918	Traces
526	Doremus, Utah	Oct. 30, 1918	Poor

Chrysothamnus nauseosus var. **frigidus**

Chemical Analysis

	Place of Collection	Date of Collection	Acetone Extract Per cent.	Benzene Extract Per cent.
271	Laramie, Wyoming	July 7, 1918	16.60	1.86

Microscopical Examination

	Place of Collection	Date of Collection	Estimated Amount
262	Near Rock Hill, Utah	June 30, 1918	Traces

Chrysothamnus nauseosus var. **gnaphalodes**

Chemical Analyses

	Place of Collection	Date of Collection	Acetone Extract Per cent.	Benzene Extract Per cent.
48	West of Lancaster, Calif.	Oct. 27, 1917	3.10	1.90
72	Benton, Calif.	Nov. 5, 1917	4.10	3.60[x]
87	West of Lancaster, Calif.	Jan. 19, 1918	2.78	0.59
203	Kearsarge, Inyo Co., Calif.	Jan. 28, 1918	2.81	1.45
215	Schurz, Nev.	Feb. 26, 1918	4.29	2.57
447	Benton, Calif.	Sept. 16, 1918	3.66	2.66
448	Benton, Calif.	Sept. 16, 1918	3.55	3.58
449	Benton, Calif.	Sept. 16, 1918	2.39	1.85
561	Basalt, Nev.	Dec. 21, 1918	3.67	0.94[x]
562	Basalt, Nev.	Dec. 21, 1918	2.88	0.95[x]
577	Near Barstow, Calif.	Dec. 24, 1918	2.12	0.26[x]
578	Near Barstow, Calif.	Dec. 24, 1918	2.71	0.88
658	Quinn River Valley, Nev.	Jan. 1, 1918	3.30	1.88
711	Near Victorville, Calif.	Dec. 26, 1918	2.27	0.96
712	Near Victorville, Calif.	Dec. 26, 1918	2.96	1.80
778	West of Lancaster, Calif.	Mar. 13, 1919	2.72	1.23
779	West of Lancaster, Calif.	Mar. 13, 1919	2.30	1.20
780	West of Lancaster, Calif.	Mar. 13, 1919	2.40	0.76

Microscopical Examinations

	Place of Collection	Date of Collection	Estimated Amount
13	Pyramid Lake Road, Nev.	June 14, 1917	Fair
35	Pyramid Lake, Nev.	Aug. 16, 1917	Good
41	Mojave, Calif.	Oct. 25, 1917	Traces
42	Mojave, Calif.	Oct. 25, 1917	Poor
49	Lancaster, Calif.	Oct. 28, 1917	Poor
51	West of Owens Lake, Calif.	Oct. 29, 1917	Traces
53	Kearsarge, Inyo Co., Calif.	Oct. 29, 1917	Good
59	Independence, Calif.	Oct. 31, 1917	Good
63	West of Bishop, Calif.	Nov. 1, 1917	Poor
481	West of Mound House, Nev.	Sept. 23, 1918	Fair
482	Pyramid Lake, Nev.	Sept. 24, 1918	Nothing

Chrysothamnus nauseosus var. **graveolens**

CHEMICAL ANALYSES

	Place of Collection	Date of Collection	Acetone Extract Per cent.	Benzene Extract Per cent.
272	Ft. Collins, Colo.	July 7, 1918	2.84	0.67[8]
278	Trinidad, Colo.	Aug. 11, 1918	2.39	0.07
279	Trinidad, Colo.	Aug. 11, 1918	2.65	1.03
280	Trinidad, Colo.	Aug. 8, 1918	3.02	0.68
281	Trinidad, Colo.	Aug. 11, 1918	2.88	0.69
283	Purgatoir River, Colo.	Aug. 15, 1918	3.13	0.36
296	Cimarron, Colo.	Sept. 1, 1918	3.15	0.21
299	Near Grand Junction, Colo.	Sept. 1, 1918	2.03	3.19
411	Near Cedar City, Utah	Sept. 5, 1918	2.03	0.49
516	Green River, Utah	Oct. 18, 1918	2.88	0.87

MICROSCOPICAL EXAMINATIONS

	Place of Collection	Date of Collection	Estimated Amount
266	Vernal, Utah	July 1, 1918	Traces
288	Cañon City, Colo.	Aug. 6, 1918	Traces
297	Grand Junction, Colo.	Sept. 1, 1918	Traces
298	Grand Junction, Colo.	Sept. 1, 1918	Traces
401	Near Grand Junction, Colo.	Sept. 2, 1918	Traces
412	Near Cedar City, Utah	Sept. 5, 1918	Poor
497	Garden of the Gods, Colo.	July —, 1918	Poor

Chrysothamnus nauseosus var. **hololeucus**

CHEMICAL ANALYSES

	Place of Collection	Date of Collection	Acetone Extract Per cent.	Benzene Extract Per cent.
62	West of Bishop, Calif.	Nov. 1, 1917	4.00	4.10
451	Benton, Calif.	Sept. 16, 1918	2.87	1.03
452	Benton, Calif.	Sept. 16, 1918	2.98	3.98
453	Benton, Calif.	Sept. 16, 1918	3.14	2.22

MICROSCOPICAL EXAMINATIONS

	Place of Collection	Date of Collection	Estimated Amount
12	Pyramid Lake Road, Nev.	June 14, 1917	Traces
34	Pyramid Lake, Nev.	Aug. 17, 1917	Fair
58	Independence, Calif.	Oct. 31, 1917	Poor
65	Benton, Calif.	Nov. 5, 1917	Poor
91	Near Palmdale, Calif.	Jan. 19, 1918	Poor
483	Pyramid Lake, Nev.	Sept. 24, 1918	Fair

Chrysothamnus nauseosus var. **leiospermus**

Chemical Analyses

	Place of Collection	Date of Collection	Acetone Extract Per cent.	Benzene Extract Per cent.
418	Near Caliente, Nev.	Sept. 6, 1918	2.82	0.84
529	Joseph City, Utah	Nov. 12, 1918	2.41	1.17[x]

Microscopical Examinations

	Place of Collection	Date of Collection	Estimated Amount
78	Near Candelaria, Nev.	Nov. 8, 1917	Traces
415	East of Caliente, Nev.	Sept. 6, 1918	Traces

Chrysothamnus nauseosus var. **mohavensis**

Chemical Analyses

	Place of Collection	Date of Collection	Acetone Extract Per cent.	Benzene Extract Per cent.
550	Mt. Hamilton, Calif.	Dec. 15, 1918	2.05	0.30[x]
551	Mt. Hamilton, Calif.	Dec. 15, 1918	2.90	0.30[x]
552	Mt. Hamilton, Calif.	Dec. 15, 1918	2.79	1.08[x]
553	Mt. Hamilton, Calif.	Dec. 15, 1918	2.15	0.44[x]

Microscopical Examinations

	Place of Collection	Date of Collection	Estimated Amount
40	Mojave, Calif.	Oct. 25, 1917	Nothing
43	Southwest of Mojave, Calif.	Oct. 25, 1917	Poor
44	Southwest of Mojave, Calif.	Oct. 25, 1917	Traces
92	Near Palmdale, Calif.	Jan. 19, 1918	Poor

Chrysothamnus nauseosus var. **occidentalis**

Chemical Analyses

	Place of Collection	Date of Collection	Acetone Extract Per cent.	Benzene Extract Per cent.
775	Near Tejon Pass, Calif.	Mar. 13, 1919	2.78	0.95
776	Near Tejon Pass, Calif.	Mar. 13, 1919	2.84	0.71
777	Tejon Pass, Calif.	Mar. 13, 1919	1.88	1.54

Chrysothamnus nauseosus var. **pinifolius**

Chemical Analyses

	Place of Collection	Date of Collection	Acetone Extract Per cent.	Benzene Extract Per cent.
290	Alamosa, Colo.	Aug. 31, 1918	4.27	3.41
291	Alamosa, Colo.	Aug. 31, 1918	4.81	1.11
293	Salida, Colo.	Aug. 3, 1918	4.05	3.98
294	Salida, Colo.	Aug. 31, 1918	4.00	2.65[x]
788	San Luis Valley, Colo.	Mar. 15, 1919	3.62	3.59

Microscopical Examination

	Place of Collection	Date of Collection	Estimated Amount
265	East of Roosevelt, Colo.	June 30, 1918	Traces

Chrysothamnus nauseosus var. **speciosus**

CHEMICAL ANALYSES

	Place of Collection	Date of Collection	Acetone Extract Per cent.	Benzene Extract Per cent.
229	South of Likely, Modoc Co., Calif.	Mar. 8, 1918	3.55	2.49
240	Near Weed, Calif.	June 6, 1918	2.43	1.52
245	Antelope, Ore.	June 16, 1918	3.83	2.77
248	Near Burns, Ore.	June 19, 1918	3.10	0.40
255	East of Hammett, Idaho	June 22, 1918	4.16	2.52
270	Rawlins, Wyo.	July 3, 1918	3.70	1.80[N]
405	Stockton, Colo.	Sept. 3, 1918	2.87	0.52
406	Stockton, Colo.	Sept. 3, 1918	2.39	0.44
407	Stockton, Colo.	Sept. 3, 1918	3.09	0.38
462	Warren Creek, Calif.	Sept. 20, 1918	3.98	0.58
465	Mono Lake, Calif.	Sept. 20, 1918	3.48	1.55
471	Near State Line Lake, Nev.	Sept. 22, 1918	3.37	0.49
495	Redmond, Ore.	Sept. 29, 1918	4.02	0.73
498	Lolo, Mont.	Dec. 4, 1918	2.75	0.77[N]
557	Reno, Nev.	Dec. 20, 1918	3.43	2.31[N]
559	Near Reno, Nev.	Dec. 20, 1918	2.31	0.62[N]
758	Spokane, Wash.	Feb. 18, 1919	3.49	0.16

MICROSCOPICAL EXAMINATIONS

	Place of Collection	Date of Collection	Estimated Amount
6	Truckee, Calif.	June 6, 1917	Traces
10	Boca, Calif.	June 18, 1917	Nothing
17	Ogden, Utah	June 19, 1917	Traces
20	Ogden, Utah	Aug. 7, 1917	Traces
21	Ogden, Utah	Aug. 7, 1917	Traces
25	Goldfield, Nev.	Aug. 10, 1917	Poor
27	Reno, Nev.	Aug. 14, 1917	Poor
37	Truckee, Calif.	Aug. 17, 1917	Nothing.
39	Reno, Nev.	Aug. 14, 1917	Poor
150	Redmond, Ore.	May —, 1918	Poor
161	Albuquerque, New Mex.	July 29, 1918	Poor
162	Modoc Co., Calif.	Nov. —, 1918	Poor
163	Modoc Co., Calif.	Nov. —, 1918	Fair
164	Modoc Co., Calif.	Nov. —, 1918	Fair
244	South of Roseburg, Ore.	June 8, 1918	Nothing
246	Near Antelope, Ore.	June 16, 1918	Traces
249	Near Burns, Ore.	June 19, 1918	Nothing
264	Near Duchesne, Utah	June 30, 1918	Traces
269	Southwest of Rawlins, Wyo.	July 7, 1918	Traces
435	Lida, Nev.	Sept. 10, 1918	Traces
464	Mono Lake, Calif.	Sept. 20, 1918	Nothing
488	Reno, Nev.	Sept. 25, 1918	Poor
501	Grantsville, Utah	Sept. 25, 1918	Poor
503	Grantsville, Utah	Sept. 25, 1918	Poor
511	Near Salt Lake, Utah	Oct. 7, 1918	Poor
512	Near Salt Lake, Utah	Oct. 7, 1918	Poor

Chrysothamnus nauseosus var. **viridulus**

CHEMICAL ANALYSES

	Place of Collection	Date of Collection	Acetone Extract Per cent.	Benzene Extract Per cent.
54	Kearsarge, Inyo Co., Calif.	Oct. 29, 1917	3.90	4.84[X]
64	Benton, Calif.	Nov. 3, 1917	3.74	5.56[X]
80	Near Benton, Calif.	Nov. 10, 1917	3.56	2.00
133	Benton, Calif.	Feb. 15, 1918	4.12	3.64[X]
134	Near Benton, Calif.	Feb. 17, 1918	3.73	2.18
211	Fish Lake Valley, Nev.	Feb. 25, 1918	5.65	2.00
212	Near Oasis, Nev.	Feb. 25, 1918	5.02	0.96
428	Beatty, Nev.	Sept. 8, 1918	2.40	2.70
434	Lida, Nev.	Sept. 10, 1918	2.57	1.67
439	Near Deep Spring Valley, Calif.	Sept. 12, 1918	2.22	2.39
441	Benton, Calif.	Sept. 16, 1918	2.80	2.31
442	Benton, Calif.	Sept. 16, 1918	3.18	3.97
443	Benton, Calif.	Sept. 16, 1918	2.52	3.11
444	Benton, Calif.	Sept. 16, 1918	2.60	3.83
445	Benton, Calif.	Sept. 16, 1918	3.13	5.29
446	Benton, Calif.	Sept. 16, 1918	3.61	4.16
450	Benton, Calif.	Sept. 16, 1918	2.50	2.09
459	Near Mono Lake, Calif.	Sept. 19, 1918	3.64	1.79
467	Near Mono Lake, Calif.	Sept. 22, 1918	3.71	1.74[X]
468	Near Mono Lake, Calif.	Sept. 22, 1918	2.88	0.65
563	Near Benton, Calif.	Dec. 21, 1918	3.38	0.52
565	Benton, Calif.	Dec. 21, 1918	2.64	0.58
570	Benton, Calif.	Dec. 21, 1918	2.92	1.09[X]
571	Near Benton, Calif.	Dec. 21, 1918	3.49	4.45[X]
572	Benton, Calif.	Dec. 21, 1918	3.04	4.00[X]
574	Near Benton, Calif.	Dec. 23, 1918	2.61	2.00[X]
576	Near Benton, Calif.	Dec. 23, 1918	6.85	3.93[X]
590	Near Victorville, Calif.	Dec. 25, 1918	2.70	2.43
704	Cushenberry Spring, Calif.	Dec. 25, 1918	3.21	1.02
705	Cushenberry Spring, Calif.	Dec. 25, 1918	2.13	1.30
706	Cushenberry Spring, Calif.	Dec. 25, 1918	2.08	1.34
718	Hesperia, Calif.	Dec. 26, 1918	1.94	0.44
748	Near Barstow, Calif.	Dec. 30, 1918	3.71	3.35
749	Near Benton, Calif.	Dec. 23, 1918	5.79	1.32
752	Mono Lake, Calif.	Feb. 1, 1919	3.47	3.75
755	Mono Lake, Calif.	Feb. 1, 1919	3.74	2.26

MICROSCOPICAL EXAMINATIONS

	Place of Collection	Date of Collection	Estimated Amount
47	Near Rosamond, Calif.	Oct. 27, 1917	Good
50	West of Owens Lake, Calif.	Oct. 29, 1917	Fair
55	Kearsarge, Inyo Co., Calif.	Oct. 29, 1917	Good
56	Kearsarge, Inyo Co., Calif.	Oct. 29, 1917	Poor
57	Kearsarge, Inyo Co., Calif.	Oct. 29, 1917	Good
60	West of Bishop, Calif.	Nov. 1, 1917	Good
79	Near Mina, Nev.	Nov. 9, 1917	Good
84	Laws, Inyo Co., Calif.	Nov. 13, 1917	Fair
88	West of Lancaster, Calif.	Jan. 19, 1918	Poor

X. DISTRIBUTION OF RUBBER IN THE PLANT

a. REGIONAL DISTRIBUTION IN THE PLANT

Since our main endeavors have been directed to an examination of a large number of individual plants of a number of species of *Chrysothamnus* and other genera, no great attention has been given to many interesting and perhaps ultimately important details which have to do with anatomical peculiarities and with the origin and occurrence of rubber, which, under other circumstances, might well have concerned us. Indeed, various causes have resulted in an accumulation of studies much less detailed concerning these matters than was originally anticipated. Again, since our interest lay primarily in discovering the average rubber content of the main rubber bearing tissues and since it was early seen that the latter were peculiar to the older parts of the stem, the younger portions of both stem and root, the study of which is necessary for a thorough elucidation of the problems of the origin and occurrence of rubber, were not usually collected in the field and were thus not available for study in many cases. At the present time, however, we are prepared to make certain general statements concerning the distribution of rubber in the plants with which we have been concerned, and leave for further description a number of matters which are still under investigation. Particularly, we aim in what follows to interpret for such persons as may concern themselves with histological examinations of plants suspected of containing rubber, the appearance of the sections which they will be likely to obtain and to indicate to them the nature and distribution of the tissues in which rubber may be expected to occur. In this endeavor we will emphasize the results of our histological studies, but will also draw upon those derived from chemical analysis.

Attention has already been called to the fact that as in Guayule, so in *Chrysothamnus* we are dealing with a non-latex rubber which is found deposited as such within the individual cells of certain portions of the plant body. It may be noted in passing that many persons, even at the present time, are not acquainted with the nature of the occurrence of rubber in Guayule, nor with the consequent processes of extraction, the latter differing so decidedly from those employed in the case of plants which bear latex-rubber. Since identical or similar processes will undoubtedly be employed should Chrysil at any time prove of sufficient importance to warrant its extraction on a

commercial scale, it may not be out of place to refer the reader to the description of the commercial process for the extraction of Guayule, given by Lloyd.[18]

With reference to the relative amounts and the general distribution of rubber in the various parts of the plant body certain points seem rather well established. This is an important matter since persons planning to extract Chrysil on a commercial scale would at the start wish to know which portions of the plant contain maximum quantities of rubber and should be harvested and which portions should be discarded as containing negligible quantities. The following table contains the results of such analyses as we have at hand bearing upon this matter.

TABLE 7.—RESULTS OF ANALYSES MADE TO INDICATE THE RELATIVE AMOUNTS OF RUBBER BORNE BY THE VARIOUS PARTS OF THE PLANT BODY—*Chrysothamnus*

Collection Number	Variety	Acetone Extract Per cent.	Benzene Extract Per cent.	Remarks
144 (1)	[1]C. n. consimilis	3.75	0.81	First 10 cm. up from end of root
(2)		3.59	2.12	10 cm. section, from first rootlets to soil line
(3)		3.69	1.74	Main branches, 4 to 8 years old at bases and 30 cm. long
(4)		4.64	1.85	Tops of branches, 3 to 4 years old at bases, 2 years old at tops
752 (1)	[2]C. n. viridulus	3.47	3.75	At soil line
(2)		11.80	1.70	2 year old shoots
(3)		22.57	0.42	Tops, 1 year old
755 (1)	[2]C. n. viridulus	3.74	2.26	At soil line
(2)		15.10	1.63	2 year old shoots
(3)		19.80	0.74	Tops, 1 year old
620 (1)	[3]C. n. consimilis	2.89	0.13	End of root, 10 cm.
(2)		3.54	0.28	Next 10 cm. up root
(3)		2.99	0.37	Third 10 cm. up root
(4)		2.89	0.43	Fourth 10 cm. up root
(5)		3.46	3.03	Soil line
(6)		2.79	1.54	First 7 cm. up from soil line
(7)		2.97	1.91	Second section up from soil line, 8 cm.
(8)		3.24	2.07	Third section up from soil line, 8 yrs. old
(9)		3.16	2.20	Fourth section, 7 years old
(10)		3.43	1.91	Fifth section, 6 years old
(11)		2.79	2.20	Sixth section, 5 years old
(12)		2.86	2.77	Seventh section, 4 years old

[1] Collected, Goleonda, Nev., Mar. 4, 1918.
[2] Collected, Mono Lake, Feb. 1, 1919.
[3] Collected, Ely, Nev., Feb., 1919.

[18] *L.c.*, p. 8.

Table 7.—(*Continued*)

Collection Number	Variety	Acetone Extract Per cent.	Benzene Extract Per cent.	Remarks
(13)		2.80	2.43	Eighth section, 3 years old
(14)		6.12	1.63	Shoots, 2 years old
(15)		13.79	1.27	Shoots, 1 year old
(16)		20.33	1.01	Tips, current year
622 (1)	[3]C. n. consimilis	4.72	0.36	End of root, 30 cm.
(2)		4.59	0.35	Next 10 cm. up root
(3)		4.26	0.48	Next 10 cm. up root
(4)		5.49	0.96	Next 10 cm. up root
(5)		2.15	1.56	Next 10 cm. up root
(6)		2.15	2.36	Soil line
(7)		3.42	2.12	Main branches, 5 to 6 years old.
(8)		2.65	1.88	Main branches, 4 to 5 years old
(9)		3.29	1.64	Main branches, 3 to 4 years old
(10)		4.52	2.39	Main branches, 2 to 3 years old
(11)		5.52	0.96	Shoots, 2 years old
(12)		10.72	0.83	Shoots, 1 year old
(13)		2.12	0.86	Tips, current year.

[3] Collected, Ely, Nev. Feb., 1919.

For convenience of discussion the table above has been differently arranged and somewhat condensed in the table which follows:

Table 8.—The Relative Amounts of Rubber Found in Various Portions of the Root and in Portions of the Stem of Various Ages

Collection Number	144	752	755	620	622
End of root	0.81			0.13	0.36
Root up to soil line (av.)				0.32	0.83
Soil line	2.12	3.75	2.26	3.03	2.36
Base of main stems, 6 years old and older	1.74			1.93	2.12
Stems, 4 to 5 years old				2.48	1.88
Stems, 3 to 4 years old	1.85			2.60	1.64
Branches, 2 to 3 years old				2.03	2.39
Branches, 2 years old		1.70	1.63	1.63	0.96
Branches, 1 year old		0.42	0.74	1.27	0.83
Tops, current year				1.01	0.86

These data indicate that in *Chrysothamnus* the root proper (below a point from six to eight inches below the soil line) contains little or no rubber. In addition to the two species for which analyses are given in tables 7 and 8 we have analyses comparing the rubber content of stem and root in the case of *gnaphalodes* and *pinifolius* which give results closely similar to those above. Attention should here be called to the fact, discussed in detail elsewhere (p. 274) that

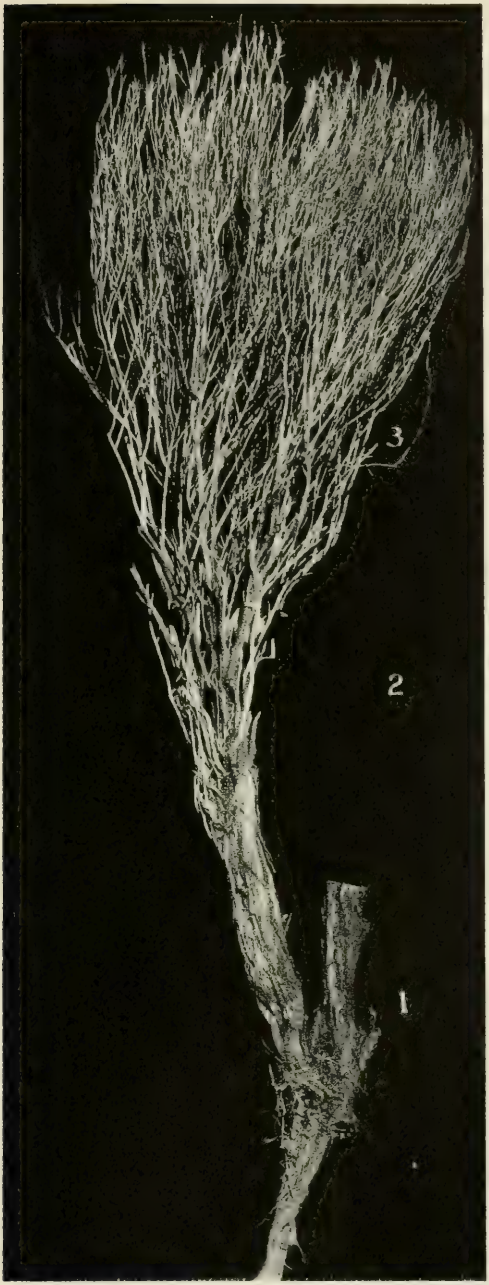


Fig. 5. A large plant of *Chrysothamnus nauseosus* var. *viridulus*. 1 indicates the assumed soil-line; 2 the upper limits of the main trunk; 3 the approximate upper limits of the three- to four-year-old wood.

in certain species of *Haplopappus* rubber is confined to the root or occurs in approximately equal amounts in root and stem.

As far as stem structures are concerned it is more difficult to indicate a sharp line of demarcation between those which are significant and those which are not significant as far as rubber content is concerned. Figure 5 shows a large plant of *viridulus* (no. 565) and serves to indicate the characteristic method of branching and the general configuration of plants of this and other varieties which we have examined.

The assumed soil line, the upper limits of the main trunk, and the approximate upper limits of the three- to four-year-old wood are shown. The results listed in tables 7 and 8 suggest that only such parts of the plant as lie between 1 and 3 contain sufficient rubber to warrant their harvesting if the plants were used as a commercial source of rubber.

In the various tables above and in those which follow, analyses of portions

of plants furnish the data on the basis of which a certain percentage rubber content is assigned to a given individual. Figure 4 shows plants trimmed for grinding and analysis and it is apparent that what is left of the plants represent areas roughly equivalent to the portion between 1 and 2 in figure 5.

It appears from tables 7 and 8 that maximum quantities of rubber occur at the soil line. In the case of future examinations of plants to get at the per cent of contained rubber it would appear that this basal portion of the main trunk alone might furnish a characteristic sample and that the whole area between 1 and 3 (fig. 5) need not be handled. In other words analysis of a soil line sample of such a plant as 620 (table 7, 620 (5)) indicated that approximately 3 per cent of rubber was present and it is held that this figure may safely be taken as a fair approximation of the per cent borne by the entire plant exclusive of the root and the shoots and twigs less than three or four years old. At first sight it would appear that this figure is too high since table 7 indicates that an average percentage content of segments (5) to (13) of 620 would approximate 2 rather than 3 per cent. In this connection, however, the relative weights of the areas between 1 and 2 (cf. fig. 5) and between 2 and 3 must be taken into account. A number of weighings indicate that the weight of that portion between 2 and 3 is approximately 30 per cent of the total weight of the region between 1 and 3. This total weight will roughly approximate 1500 grams. It appears from the data given that if the main trunk bears in the neighborhood of 3 per cent the branches up to the limits of the three to four year old wood will bear about 2 per cent. With this assumption in mind the following relation appears to hold good:

Weight 1 to 2 = 1150 gm., which at 3% = 34.50 gm. rubber.
Weight 2 to 3 = 450 gm., which at 2% = 9.00 gm. rubber.

Total weight = 1500 gm., total rubber = 43.50 gm.
Total weight = 1500 gm. at 3% = 45.00 gm. rubber.
Total weight = 1500 gm. at 2% = 30.00 gm. rubber.

Based upon such rough estimates as these it seems clear that, due to the greater weight of the main trunk as compared with the older branches, a report of per cent of contained rubber based upon an analysis of portions of the plant near the soil line would not give a wholly erroneous estimate of the amount of rubber to be obtained from a plant harvested so that parts from 1 to 3 (fig. 5) alone were retained.

As stated above we have been unable to secure a sufficiently large number of analyses of the younger and older portions of plants to make our conclusions as to regional distribution of rubber entirely authoritative. The surprising decrease in rubber content a short distance above the soil line is perplexing as is the succeeding increase in the upper portion of the main trunk and branches. Elimination of the primary cortex by peridermal activity in the older trunk elements is obviously not an adequate explanation since at the soil line maximum elimination of cortical tissue has taken place. Indeed, cork formation with the accompanying distintegration of rubber cut out thereby has progressed to a decided extent before the third year of growth. The results obtained suggest, among other things, a translocation of rubber or its derivatives. Such implications deserve nothing more than a mere mention when the data are so fragmentary.

b. SPECIFIC DISTRIBUTION IN MATURE TISSUES

In an earlier paragraph it was stated that for making a rough estimate under the microscope of the amount of rubber borne by a given plant, a piece of mature tissue was cut from the main stem axis. For convenience we may use as the basis for a description of the tissues in which rubber, if present, may be expected to occur, the accompanying photomicrographs and photographs of stained preparations. As will be noted in plates — and — the stained areas are for the most part extracambial although the rays are also conspicuously stained. Analyses of one plant indicate that the amount of rubber in the cortex as compared with that in the woody cylinder is in the ratio of approximately six to one.

Not all the stained areas without the cambium are rubber bearing, however. Sudan III stains intensely the walls of corky tissues and the superficial portions of the stained material outside the woody cylinder represent cork and bark. Within this outermost layer the broad wedge-shaped extensions of the primary rays are most conspicuously stained. In a plant bearing from 4 to 5 per cent of rubber all the cells of these ray extensions are filled with rubber inclusions. Indeed in microscopical examinations of *Chrysothamnus* these areas should first be examined for the presence of rubber as, uniformly, in sections of stems over two years old, stainable rubber inclusions, if present at all, will here be found.

Bands of stained tissue will be seen connecting tangentially the cortical ray extensions. These represent the parenchymatous elements

of the cortex and non-functional phloem increments. The functional phloem areas are also rubber bearing although in this case the protoplasmic matrices of the cells often stain in simulation of rubber inclusions. The sieve tubes and companion cells are quite small in cross-sectional diameter and only in longitudinal sections can rubber globules be identified within them. The phloem parenchyma bears the largest amount of rubber in the phloem area and even in cross-sectional view there is no difficulty in identifying the stained inclusions as such.

The cambium appears consistently to bear rubber inclusions in stems more than one year old. The rubber is in the form of small globules which seem to increase in number during cambial activity. As an annual cambium increment toward the periphery begins to become differentiated into characteristic phloem elements these small globules tend to agglomerate. Intracambially, however, the partially differentiated xylem elements contain no rubber inclusions although originating from the same rubber bearing cambium which passes on its rubber inclusions to the developing phloem increments. This situation might furnish a starting point for investigations on the chemical or physical constitution of the protoplast which is specific for the differentiation of rubber inclusions or essential for the permanence and persistence of such inclusions. In none of the mature xylem elements, parenchymatous or otherwise, have rubber inclusions been found.

Under the microscope one of the most conspicuous features which attracts attention when preparations such as those shown in plates 18 and 19 are examined is the increase in rubber deposition at certain points along the rays. Although this matter is not well brought out in all the photographs it may still be seen that at points corresponding to the spring wood of each annual xylem increment the amount of rubber is less than at those points along the rays which correspond to the summer or fall wood. This situation will be mentioned elsewhere in connection with a discussion of seasonal variation in rubber content.

Plates 18 and 19 (exclusive of figures 4 and 5) show cross sections of stems of various ages. The stem of the current year shown in plate 18, figure 1, is included to call attention to the deep staining of the chlorenchyma, the absence of stainable substance in cortex and rays, and especially the large quantity of stained rubber in the xylem intrusion of an axillary bud. The three year old stem in plate 18,

figure 3, illustrates the statements made above as to the conspicuous staining of the cortical ray extensions and the presence of rubber in the phloem and rays. It will be noted that the portions of the rays lying in the first annual increment contain relatively negligible amounts of rubber as compared with the portions of the rays lying in the second and third year xylem. The line "C" marks the approximate limits of the living cortex.

Figure 2 in plate 18 is included to show the extent of the rubber bearing tissues and of the non-rubber bearing cork and barky elements. The "A" line indicates roughly the external limits of the rubber bearing cortex. Cork has formed below this line but the primary cortical tissues cut out thereby show rubber not yet entirely disintegrated. The "B" line points to the tangential strip in which maximum quantities of rubber occurring in the cortical parenchyma and in the cortical ray extensions may ordinarily be expected to occur. Figure 2 is a cross section of a five year old stem.

In plate 19 the two cross sections give evidence as to the distribution of rubber in mature stems. Figure 1 was cut from a six year old stem and figure 2 from a nine year old stem. The greater portion of the bark and inner cork is absent in figure 1 and it will be seen that the cortical ray extensions filled with rubber extend outward for a long distance. The broad ray extension on the extreme left in figure 1 is characteristic of many of the cortical extensions of the primary rays and its cells are densely packed with rubber.

Figure 2 in plate 18 shows a particularly thin section from which in places the rubber inclusions have fallen or have been washed out. Line "A" indicates roughly the limits of the rubber bearing tissues; those external being composed largely of cork and bark.

We have found that rubber is present in the cell either in what may be spoken of as a "diffused" state or in the form of globules. In the diffused state the entire cell cavity is filled with a mass of stained substance which appears to be somewhat homogeneous. This condition is shown in certain of the cells in plate 18, figure 4, the spherical globules representing detached masses of rubber which have rounded up when free from the cell wall. When present in globular form, one or more large spherical globules partially fill the cell cavity or a number of smaller definitely spherical globules are distributed without apparent arrangement within it. Spherical globules *in situ* are shown in a number of the cells in plate 18, figure 5. For a time it seemed possible that the form in which the rubber occurred in the

cell might serve as one of a number of bases for species differentiation in *Chrysothamnus*. Certainly *C. teretifolius* (cf. p. 266) consistently exhibits rubber only in the form of large spherical globules which usually occur singly and almost exclusively in the cells of the cortical

Fig. 6. Portion of a cross-section of a mature leaf of *Chrysothamnus nauseosus* var. *consimilis*. Plant grown in the University of California Botanical Garden, Berkeley. Photo-micrograph.

parenchyma. In the *nauseosus* group a number of globules often are present in the cells of young rubber bearing tissues but they tend to agglomerate with age so that the corresponding tissues when mature show few if any globular rubber inclusions, this substance being present in the "diffused" condition. Such a condition does not obtain

for *teretifolius*, globules only being found both in younger and older elements. The cross section of a leaf of a plant grown in the University of California Botanical Garden is shown in figure 6. The dark stained rubber globules in the palisade cells are conspicuous. Lloyd[18a] reports that a single large globule of rubber was characteristic of each palisade cell in certain portions of the leaf in Guayule. A corresponding condition holds for *Chrysothamnus* although in some instances it appears that more than one globule may occur in a single palisade cell. Various problems dealing with the origin of rubber and its distribution in younger tissues have been investigated in a preliminary way, at least. The results of these studies will be published in the near future as the fourth paper of the present series.

XI. FACTORS INFLUENCING RUBBER CONTENT

a. VARIATION WITH THE BOTANICAL VARIETY

The results of our studies, more particularly the chemical and microscopical examinations, indicate that rubber is present in only a few of the major species of *Chrysothamnus*. The species examined and in which it was not found with certainty are: *C. Greenei, C. Howardi, C. nevadensis, C. Parryi, C. humilis, C. puberulus,* and *C. viscidiflorus*. In *C. linifolius*, which is perhaps only a variety of *viscidiflorus,* it was found to the extent of 1 per cent in one sample but was lacking in another. The species of *Chrysothamnus* now known to yield rubber are *C. nauseosus, C. turbinatus, C. teretifolius,* and *C. paniculatus*. The last three of these are discussed elsewhere since they are of minor importance and the product is not Chrysil.[19]

Coming now to a consideration of *C. nauseosus*, we find that this variable and widespread species breaks up into about twenty-two varieties. It may be predicted with reasonable certainty that Chrysil will be found in all of these twenty-two forms. This statement is based upon the fact that of the thirteen thus far investigated every one has yielded a greater or less amount of this substance. It might be assumed, *a priori*, that certain of these botanical varieties would carry a consistently higher percentage than others. This assumption is borne out to some extent by the analyses, as is indicated in the following summary of the analytical tables published in detail on pages 226 to 233.

[18a] *L.c.*, p. 184.

[19] See pp. 265–268.

SUMMARY OF TABLE 6

	Variety	Number of samples analyzed	Rubber in poorest sample Per cent.	Rubber in best sample Per cent.	Average of all samples Per cent.
1	consimilis	69*	0.39	6.57	1.97*
2	viridulus	36	0.44	5.56	2.52
3	gnaphalodes	18	0.26	3.60	1.61
4	speciosus	17	0.16	2.77	1.18
5	graveolens	10	0.07	3.19	0.83
6	pinifolius	5	1.11	3.98	2.95
7	hololeucus	4	1.03	4.19	2.83
8	mohavensis	4	0.30	1.08	0.53
9	occidentalis	3	0.71	1.54	1.07
10	leiospermus	2	0.84	1.17	1.00
11	frigidus	1	. . . .	. . .	1.86
12	nauseosus (typical)	2	(microscopical examination only)		traces

*Others included in the complete table are here omitted since the samples were imperfect.

In making use of this table it is better to take into account only the first five varieties since the others are not represented by a sufficiently large number of samples to render the results dependable. "Individual variation" is an important factor and it is only after a large number of samples from widely separated localities have been analyzed that one is justified in drawing conclusions.

Taking then only the first five varieties it would seem that they would stand, as to rubber content, in the order of *viridulus*, *consimilis*, *gnaphalodes*, *speciosus*, *graveolens*. While this may be of significance, it is also to be noted that the first two are inhabitants of alkaline flats, the next two belong to non-alkaline slopes, and the last (as far as our samples are concerned) to only moderately if at all alkaline soil. It may be, therefore, that an apparent parallel between rubber content and botanical varieties is, in fact, due to environmental factors.

While, as just shown, there is no direct evidence that the botanical varieties represent hereditary units, each with a different capacity for rubber production, there is nothing, on the other hand, to indicate that each variety may not itself be composed of several or even numerous biotypes. If this is the case, then the separation of these through selection might lead to the discovery of a superior strain. The notable fluctuation in the rubber content of any one variety might seem to indicate this possibility but the alternative as to the influence of environment must also be kept in mind.

b. VARIATION DUE TO ENVIRONMENT

Attempts have been made to correlate the differences in the rubber content of individual plants with various factors of the environment. This has not led, as yet, to positive conclusions. One reason for the failure to obtain definite results is the low percentage in even the best plants, so that any slight variation in the selection, preparation, or analysis of any two samples might more than offset any original difference in their composition. Only through extensive experimental work, can conclusive results be hoped for.

Notwithstanding the difficulties just mentioned, a few observations may be permitted. The water content of the soil is often considered to exert an influence on rubber deposition in plants. Specimens of a single variety of *Chrysothamnus nauseosus* selected to determine this point did not vary widely in the amount of Chrysil present. There was, if anything, a slight balance in favor of those growing on moist banks but this difference was so slight that it is probably of no significance. However, when different varieties are considered, and only the average of a large number of samples taken into account, it is found that those varieties which inhabit the moist and poorly drained valley bottoms contain rubber in larger amounts than do the varieties of the very arid and well drained surrounding slopes.

This is indicated by the table on page 244. The varieties there numbered 1, 2, and 6 are lowland forms and these run higher in rubber content than do numbers 3, 4, 8, 9, 10, 11, and 12, which are upland forms. The single apparent exception to this rule is number 7, but this may be due to the small number of samples analyzed for that variety.

But, while the formation of rubber thus seems to be favored by the more abundant moisture of the lowlands, another factor may be the real cause of the increase in percentage, namely, the presence of alkali. It is not impossible that the alkali acts indirectly through the water relation. It is well known that its presence reduces the amount of water available to plants, and it is conceivable that by thus lowering the chresard it causes a deficiency in physiological moisture which is even greater than the deficiency on the surrounding slopes. However this may be, it is certain that the best rubber producing varieties of *Chrysothamnus nauseosus* are those of the alkaline valley bottoms.

As to temperature, it seems unlikely that this factor exerts an influence on rubber formation except as it acts through other agencies.

There is no striking difference between the percentages found in the plants from the hot desert valleys of California and the cold mountain valleys of Colorado. The apparent running down of rubber content as one approaches the limits of distribution for the species is perhaps to be accounted for on other grounds. If temperature were the controlling factor it would be difficult to explain the uniformly low rubber content of plants from the warm Coast ranges of California and also of the cool plateaus at the eastern base of the Rockies.

The effect of wounds and of pruning may be a matter of much importance in case the plants are ever brought under cultivation. The wild shrubs are often riddled by the attacks of larvae and beetles, but their influence, if any, is not known. Experiments now in progress have already determined that the plants may be pruned back without injury and that this greatly increases the number and weight of the rubber bearing stems. The possible effect upon the formation of rubber will be determined later. (See plate 20.)

c. SEASONAL VARIATION

In the case of Guayule a variety of evidence points to the fact that there exists a striking seasonal variation in rubber content. Thus, it has been found that during the active season of growth only negligible quantities of rubber are deposited while during the following resting period rubber makes its appearance in the tissues. These two periods are correlated with the duration of the rainy season in the desert region where Guayule grows wild. During the rains growth is initiated and continues for a time. Shortly after the start of the dry season active vegetative growth ceases and rubber then begins to be deposited in the recently formed tissues.

With these facts in mind some experiments were made to determine whether a similar situation holds for rubber deposition in *Chrysothamnus*. Table 9 gives the results of these experiments. On September 16, 1918, portions of mature tissues were cut from thirteen plants representing three different varieties of *nauseosus* growing in a small tract near Benton, California. Notes and photographs made it possible on December 22, 1918, to remove from the same plants portions apparently equivalent to those which had been secured in September. There was no evidence that the removal of the first portion had in any way impaired the remainder of the plant or impeded its normal development. The September date is taken to represent the close of the growing period at which time the flowers

are produced. By the end of December the resting period is practically at an end since shortly thereafter the early spring growing season begins.

TABLE 9.—SEASONAL VARIATION IN RUBBER CONTENT OF THREE VARIETIES OF *Chrysothamnus nauseosus*

(September 16, 1918, represents the close of the growing season and December 22, 1918, the close of the resting season.)

	Variety	Place of Collection	Date of Collection	Acetone Extract Per cent.	Benzene Extract Per cent.
441	C. n. viridulus	Benton, Calif.	Sept. 16, 1918	2.80	2.31
		Benton, Calif.	Dec. 22, 1918	3.16	2.86
442	C. n. viridulus	Benton, Calif.	Sept. 16, 1918	3.18	3.97
		Benton, Calif.	Dec. 22, 1918	3.58	3.77
443	C. n. viridulus	Benton, Calif.	Sept. 16, 1918	2.52	3.11
		Benton, Calif.	Sept. 16, 1918	2.18	3.27*
		Benton, Calif.	Dec. 22, 1918	2.82	3.06
		Benton, Calif.	Dec. 22, 1918	2.97	2.95*
444	C. n. viridulus	Benton, Calif.	Sept. 16, 1918	2.60	3.83
		Benton, Calif.	Dec. 22, 1918	2.80	2.63
445	C. n. viridulus	Benton, Calif.	Sept. 16, 1918	3.13	5.29
		Benton, Calif.	Dec. 22, 1918	3.13	3.49
446	C. n. viridulus	Benton, Calif.	Sept. 16, 1918	3.61	4.16
		Benton, Calif.	Dec. 22, 1918	3.87	3.97
447	C. n. gnaphalodes	Benton, Calif.	Sept. 16, 1918	3.66	2.66
		Benton, Calif.	Dec. 22, 1918	3.43	1.52
448	C. n. gnaphalodes	Benton, Calif.	Sept. 16, 1918	3.55	3.58
		Benton, Calif.	Dec. 22, 1918	4.76	3.95
449	C. n. gnaphalodes	Benton, Calif.	Sept. 16, 1918	2.39	1.85
		Benton, Calif.	Dec. 22, 1918	2.79	0.99
450	C. n. gnaphalodes	Benton, Calif.	Sept. 16, 1918	2.50	2.09
		Benton, Calif.	Dec. 22, 1918	2.63	1.65
451	C. n. hololeucus	Benton, Calif.	Sept. 16, 1918	2.87	1.03
		Benton, Calif.	Dec. 22, 1918	3.44	0.79
452	C. n. hololeucus	Benton, Calif.	Sept. 16, 1918	2.98	3.98
		Benton, Calif.	Dec. 22, 1918	4.77	4.06
453	C. n. hololeucus	Benton, Calif.	Sept. 16, 1918	3.14	2.22
		Benton, Calif.	Dec. 22, 1918	3.98	2.12

*Duplicate analysis.

It seems probable from the results listed above that during the resting period the resins and other acetone-soluble substances increase in amount while the amount of rubber is diminished. This situation is unexpected in view of the reverse condition described above for Guayule. It is, also, of particular interest when the influence of storage of shrub upon resin and rubber content is recalled (cf. p. 224). In the case of storage the per cent of resins was considerably reduced along with a slight reduction in per cent of rubber. Obviously there

is need of further experiments and analyses to confirm the results of the more or less preliminary experiments tabulated above. Indeed a few exceptions to our general conclusion appear in table 9 and while not numerous enough to affect it materially certainly cast some doubt upon it. It is entirely possible that in selecting the two dates for collection of samples the critical period may have been overlooked. Thus, if a sample had been taken in August or earlier as well as in September a decided increase in rubber content might have been noted for the latter date. This would have meant that the flowering period in *Chrysothamnus* represents, in terms of seasonal variation in rubber content as observed for Guayule, not the end of the growing period but the beginning of the resting period during the start of which maximum deposition of rubber takes place very rapidly.[20] Had such collections been made and such results obtained no light would, however, have been thrown upon the seeming disappearance during the resting period of a certain proportion of the rubber present within a month of its start.

XII. METHODS OF HARVESTING: SEASON, AGE, DEPTH OF CUTTING, ETC.

The methods of harvesting have not been worked out in detail since it has not been demonstrated that *Chrysothamnus* can be utilized on a commercial scale. However, our preliminary studies have indicated certain general principles to be observed in case rubber is ever prepared from the plants and they are here set forth as follows.

The question of the distribution of rubber in the various plant organs and the extent of its occurrence in stems of various ages is discussed elsewhere (cf. p. 234). It may here be said that the amount of rubber in parts less than three years old is relatively small. From the third year onward for one or two years the amount increases rather rapidly. After the fifth or sixth year the quantity of rubber present remains more or less constant. The cause of this constancy in amount depends upon certain facts taken up in detail elsewhere. In the first place, the extracambial tissues are almost the exclusive regions of rubber deposition. Secondly, when cork formation takes place there is, each year, an amount of rubber containing cortical tissue cut off which roughly approximates the amount of new cortical tissue annually

[20] The microscopical evidence (cf. p. 240) appears to give a partial confirmation of such a supposition.

laid down. Finally, with the appearance of the phellogen deep in the cortex and the production by it of a few layers of cork the rubber in the cells external thereto begins to degenerate and soon loses its characteristic staining capacity. It is true, of course, that the annual increments added intracambially to the primary medullary rays and which in part are devoted to the origination of secondary rays increases each year the number of cells in the woody cylinder available for rubber deposition. There is in this case, obviously, no such annual reduction in the amount of rubber bearing tissues as is characteristic of the cortex. The amount of new rubber bearing tissue added each year to the existing ray material is so small and the quantity of rubber present in the individual ray cells is so relatively diminutive, that this source of increase in the rubber content of old as compared with younger stems is negligible.

The problem of a seasonal or periodic deposition will require for its final solution a much more detailed study than we have been able to give to it. The experiments mentioned on page 246 seem to indicate that the maximum amount of rubber is present near the close of the growing season. If these results are confirmed they will have a directive influence in determining the season at which harvesting should take place. This probably would not be a determining factor in selecting the season for harvesting wild shrub, but it might mean the difference between financial success and failure when the handling of cultivated plants is under consideration.

It would follow from the foregoing that old plants would be the best rubber producers. It is evident that as the plant becomes overmature decay sets in and reduces the weight of the rubber carrying portions. This is borne out to some extent by the results of our analyses, which indicate that the average percentage composition is about the same for large old plants as for medium sized plants of moderate age. Young plants, say four years old or less, are almost always low in percentage content, a direct result of the fact that deposition is small until about the third year and the ratio of rubber bearing tissue to the whole plant is therefore low. This discrepancy gradually disappears with age. It is quite certain that shrub which has reached maturity, that is, six to ten years for the *viridulus* form, bears its maximum quantity of rubber.

The depth at which the plants may be cut in harvesting without destroying the power of regeneration is a matter which has received considerable attention because of its practical bearings. Histological and

chemical analyses of the root indicate that it carries its highest percentage of rubber at about the surface of the soil and that the percentage rapidly diminishes downward, until at an average depth of about four inches the amount present is so small that the remainder of the root is of no value. In harvesting, it would therefore be desirable to make the cut about four inches below the surface. Our experiments, performed on over three hundred plants of three leading varieties, have definitely determined, however, that if this is done, or if the root is cut off anywhere below its junction with the stem, the portion remaining in the soil will die. The obvious explanation of this phenomenon is that, as in most plants, new shoots arise only from stem tissue. In all cases where the stems were cut off just above the soil surface the stumps promptly sent up an abundant growth of new shoots. In one case a diagonal cut was made just at the surface so that about an inch of stem was left on one side of the stump, while on the opposite side the cut extended to about an inch below the top of the root. After a lapse of six months there was a copious growth of shoots two feet long from the higher side of the stump, none at all from the lower.

The line of demarcation between stem and root is not a sharp one. A microscopic examination for dormant buds is, of course, impractical in field work; the bark is so similar on the lower part of the stem and the upper part of the root that its texture and color furnish no clue; and the soil level cannot be accepted as a criterion since it is easily modified by disturbing agencies such as erosion, deposition, accumulation of vegetable matter, and the activities of rodents. In most cases, a cut made just at the first crotch, which is usually also at the original soil surface, will safely provide for regeneration but much experience will be necessary if one desires to obtain the maximum amount of rubber and at the same time be assured of new growth without replanting. In case the wild shrub is ever utilized for an emergency supply of rubber it will probably be best to make the cut at about six inches below the surface, thus sacrificing the roots for the sake of the rubber in their upper portions; on the other hand, if *Chrysothamnus* is grown as a field crop it will probably be found profitable to provide for vegetative reproduction, either by leaving an inch or so of stem or by leaving portions of several of the lower branches as a foundation for a larger and broader plant.

The bulk of the shrub may be materially reduced without much loss of rubber by cutting off and discarding all growth less than three

years old. Wood which is just in its second year may or may not be worth preserving, depending upon methods of milling, local conditions, and the value of the rubber. The age is easily determined in young stems by counting the growth rings. The color and texture of the bark may also be used as a guide by one familiar with the plant. The removal of all growth of less than three years will take with it all of the leaves, but these, like the twigs themselves, carry only traces of rubber.

XIII. POSSIBILITIES OF *CHRYSOTHAMNUS* AS A CULTIVATED PLANT

It is eminently desirable that a portion of the rubber consumed in the United States should be produced within our own borders. It is the only important commodity essential to modern warfare which we have not yet learned to produce. If the industry of rubber growing were once established, even though it yielded only a fraction of our normal needs, we could, through economy in use and through governmental encouragement in war time, render ourselves independent of other nations, who might refuse to supply our needs or who might be unable to transport their products across the seas.

These same arguments can be advanced for the support of investigations looking to the production of synthetic rubber and there is no doubt that this line of work should also be encouraged. It is even possible that the synthetic product will in time replace that from the plantations. We are not in a position to forecast what the future may bring forth in this connection, but the opinion of those best capable of judging seems to be that high grade synthetic rubber in large quantities is something which we need not expect for a long time to come, if at all. In the meantime, dependence must be placed upon importations unless we can discover some commercially profitable method of growing rubber plants in our own country. The list of plants to be considered in this connection is a long one. It includes various exotics some of which are now grown in foreign countries for their rubber but none of which have been given a conclusive trial here. Certain of our native latex bearing plants, such as the milkweeds, spurges, dogbanes, etc., are now under investigation by the Carnegie Institution of Washington with some promise of success.[21] The Pinguay, or Colorado

[21] Carnegie Inst., Wash. Year-book no. 17 (1918), p. 297.

Rubber Plant (*Hymenoxys floribunda utilis*) has been unsuccessfully tried and the Guayule, a shrub native to our southern borders and to Mexico, is now under trial in Arizona. Since none of these rubber plants has as yet been agriculturally established in the United States it would seem worth while to give attention also to *Chrysothamnus* as a possible plant to be brought under cultivation for its rubber.

If a further incentive is needed for the study of rubber plants suitable to our conditions it may be found in the extent of unused and apparently unusable lands that are still to be found in our western states. The introduction of new agricultural industries for the proper utilization of these practically idle lands is one of the most important problems that now confront the people of the arid West. While we hesitate to predict that they will ever be used for the production of rubber, yet that this is within the realm of possibility is evidenced by the planting of a considerable acreage to Guayule in southern Arizona in 1918 by one of the leading rubber companies.

Guayule is a small Mexican shrub belonging to the same botanical family as the Rabbit-brush, although not very closely related to it. The similarity between the two is such that a consideration of the Guayule situation may furnish some evidence as to the possible worth of *Chrysothamnus*. The wild Guayule yields a "rubber" which had been imported into the United States in considerable quantity[22] before the political troubles in Mexico interfered with the industry. The supply of wild shrub was constantly on the wane, which led to extensive experiments in propagation, selection, breeding, and cultivation. The wild plants carry an average of 10 per cent of "Guayule gum," as it is called, but when they were brought under cultivation it was found that some plants yielded only 2 or 3 per cent, and in some cases less than 1 per cent, of pure rubber. The application of scientific methods of breeding and selection, together with the control of environmental conditions of growth have now brought the yield to as high as twenty-seven per cent in a few plants. We understand that these high percentage strains are not suitable for field growing but that those selected for planting on a large scale yield about fifteen to seventeen per cent of rubber in their fifth or sixth year.

These experiments with Guayule extended over a ten-year period and are said to have cost one company alone in the neighborhood of $500,000. Their promise, however, may be inferred from the present intention of the company to undertake planting in Arizona on a large

[22] (19,000,000 pounds in 1911.)

scale. Whether or not *Chrysothamnus* could be "improved" to the same extent is a question which we are unable to answer, for the two plants are so different in their life histories that methods used successfully with one might entirely fail with the other. Nevertheless it seems logical that the possibilities of both should be tested out before either one is exclusively selected for cultivation, since each possesses certain advantages which the other does not have. It is in order to draw a comparision between the two that the history of the introduction of Guayule into cultivation has been briefly outlined above.

The great superiority of Guayule lies in its high rubber content. As stated above, this averages ten per cent for wild plants as against an average of only 2.5 per cent for the *viridulus* form of *Chrysothamnus*. These figures are based upon pure dry rubber and dry shrub. Guayule, moreover, has been extensively studied; its habits, and its response to treatment, are at least somewhat understood, and the work thus far done upon it has resulted in the development of a fifteen to seventeen per cent strain. The improvement of *Chrysothamnus* could undoubtedly be brought about, at least to some extent, by selection and breeding. However, since it is presumably a cross fertilized plant, the separation of superior strains would be a more difficult matter than in Guayule. A starting point is indicated in that certain individuals of the variety *consimilis* actually ran as high as 6.7 per cent.

Guayule has a still further advantage in that the methods of field management, of milling, and of marketing are also established and the product is well known to the rubber trade. Here, however, the advantages of Guayule over *Chrysothamnus* seem to end.

As an offset against the above more favorable attributes of Guayule, and especially the higher rubber content, we find a number of points in favor of *Chrysothamnus*. These are here set down in order that the Mexican plant may be used to some extent as a gauge in measuring the possibilities of the other one.

(1) *Chrysothamnus* is a larger plant than Guayule, the wild shrubs averaging six pounds of rubber carrying wood, whereas the plants of the latter weigh one-half to three pounds, rarely attaining to six pounds.

(2) *Chrysothamnus* is a native of the western United States and is therefore adapted to our conditions. It grows where the temperature falls to zero and probably much lower, since it ranges up the mountains to over 7000 feet altitude. In the *consimilis* form it is known to grow over large areas where the temperature not infrequently

reaches − 20° F. Guayule, on the other hand, is too tender for any but our warmer valleys and even there its cultivation is apparently attended with some risk. Its introduction into this country is an extension of its natural range, whereas the cultivation of *Chrysothamnus* would be merely the utilization of a native plant adapted by nature to our region.

(3) *Chrysothamnus* is very resistant to alkali, often growing on soils too alkaline for any ordinary agricultural crop. It could therefore be grown on land not now utilized and which could be obtained for a very moderate price. Guayule is sensitive to alkali.

(4) The water requirement of *Chrysothamnus* is considerably less than that of Guayule. It could certainly be grown without irrigation on the cheap lands mentioned in paragraph 3.

(5) The product is superior to that of Guayule (see p. 188). It would bring a higher price in the market and if need arose would more nearly replace the fine imported rubbers in our industries.

(6) *Chrysothamnus* is more easily and cheaply propagated, both from seed, which form in abundance and are easily germinated, and vegetatively. Both old plants and seedlings may be transplanted without loss.

(7) Certain cultural practices have been developed in connection with Guayule that result in an increased yield of rubber, and methods of operation have been devised that permit of cheap handling through the use of machinery, so that the crop is said to be "machine-grown." There is no reason to suppose that similar practices and methods cannot be perfected for *Chrysothamnus*. The larger size of the shrubs and their habit of throwing up numerous new shoots when cut back indicate the possibility of increasing the tonnage of rubber carrying shrub by the cutting back of the tops (see pl. 20). Experimental work along these lines has not yet progressed to a stage where estimates would be warranted, but it is believed that a method can be worked out that will multiply by a considerable factor the tonnage of shrub per acre-year. It is possible that such manipulation may at the same time favor an increased formation of rubber in the tissues.

It would seem, therefore, that the possibilities of *Chrysothamnus* as a cultivated rubber plant should be looked into more closely. Any species which gives even the least promise should be thoroughly studied in order to find, if possible, a new crop that will turn our waste lands into productive fields and at the same time safeguard the nation against a possible deficiency in rubber during critical periods. These investi-

gations, as applied to *Chrysothamnus*, should be along several diverse lines, yet all leading to the same objective. They should include the following: detailed studies of wild plants for the purpose of discovering, if possible, better varieties or strains than we now have; garden experimentation in breeding and selection; modifications in environment, especially changes in the water relation, and the effect of methods of cultivation; the effect of varying amounts of alkaline salts on rubber deposition; and, finally, pruning and other experiments designed to test the possibility of increasing the amount of rubber bearing tissue and also of increasing the percentage in the tissues.

XIV. CULTURAL REQUIREMENTS

In case *Chrysothamnus* is brought under cultivation, its cultural requirements would need to be looked into very closely. At present, our knowledge of these is based upon observations of the wild shrub and upon a limited number of experiments in transplanting and in growing from seed.

These plants are not exacting as to their climatic requirements. The *viridulus* and *consimilis* forms grow readily from the lowest to the highest limits of the Upper Sonoran Life Zone and exceed these limits slightly in both directions. Expressed in another way, they range from fairly hot interior valleys, where the temperature runs to 110° F. in summer, to over 7000 feet in the mountains where snow falls to a depth of several feet and the temperature drops to −20° F. in winter. No difficulty has been experienced in growing these varieties in the botanical garden at Berkeley, California, both from seed and from root transplants, but it is doubtful if they will grow here as rapidly or as large as they do under conditions of greater summer heat. Transplanted seedlings are also growing at the Citrus Experiment Station at Riverside, but they are not at all vigorous. It is not known whether this is due to the very unfavorable climatic conditions that prevailed when they were set out in the field or to some other factor. Moreover, Riverside is in the Lower Sonoran Life Zone and therefore perhaps too hot in summer for these Upper Sonoran plants. While the exact geographic limits for the cultivation of *Chrysothamnus* will need to be determined with some accuracy it seems reasonably safe to say that, as far as climate is concerned, it may be grown in any of the larger interior valleys of the West except perhaps those of the extreme north and the very hot Lower Sonoran valleys of the extreme south.

The moisture and soil requirements have not been carefully determined. As indicated above the most promising forms grow on valley bottoms where there is a moderate amount of moisture and where the soil is moderately to strongly alkaline. Salt-grass (*Distichlis*) is so common a concommitant of *viridulus* and *consimilis* that its presence undoubtedly indicates favorable soil conditions. That the plants can be grown with a minimum of precipitation is indicated by their abundance in places where the precipitation drops to below two inches in some years, but in these places it flourishes only on valley bottoms. The soil is always more or less sandy, but the plants grow readily, or at least make a satisfactory start, in the heavy clay of the botanical garden at Berkeley.

An ecologic consideration always to be kept in mind is that *Chrysothamnus* is not a strong competitor among plants. It is easily crowded out by other species, especially by Grease-wood if the alkali content of the soil is high and by Sage-brush if the alkalinity is slight, so that the area at present covered by it could be greatly extended through the removal of these more aggressive shrubs. That this is true as regards Sage-brush is attested by the experience of settlers who find that Rabbit brush (especially the gray forms, *e.g.*, *gnaphalodes*) almost always takes immediate possession of the ground after the removal of the Sage-brush. This leads to the conclusion that the present occurrence of Rabbit-brush does not by any means represent the total area suited to its growth. It also indicates one rather simple method of extending the growth of the shrub, namely by removing its competitors.

In case the cultivation of *Chrysothamnus* is ever made a commercial success, the first plantations will presumably be located where the best varieties now grow wild. Aside from the assurance that such locations would provide the climatic, soil, and other requirements for successful growth, this would enable the management to utilize the wild shrub as a supplementary supply of crude rubber, although it would, of course, carry a lower percentage than the improved cultivated strains.

It is perhaps premature even to suggest districts where plantations might be located but the mention of a few may be not without interest. In Owens Valley, California, for example, it happens that the city of Los Angeles owns nearly 200,000 acres of land, partly covered with *Chrysothamnus* and not at present utilized except to a very limited extent for grazing purposes. It is estimated that at least one half of this is suitable to the growth of *Chrysothamnus* of the *viridulus* form.

Similarly, large suitable areas now partly covered with Rabbit-brush are located in Fish Lake Valley, Big Smoky Valley, Walker River Valley, near Mono Lake, and elsewhere in Nevada and eastern California. In Utah and in Colorado (especially the San Luis Valley) there are extensive tracts of practically waste land where the varieties *consimilis* and *pinifolius* are abundant. Finally, the Sacramento and San Joaquin valleys of California include large acreages of practically unused alkali lands where, unless the summer heat is too great, *Chrysothamnus* could probably be grown.

Chrysothamnus is thus seen to be a hardy plant capable of growing under a considerable range of climatic and soil conditions. It is apparently best suited to the alkaline plains of the Great Basin, especially if the soil is somewhat sandy. This fact, together with certain other practical considerations, would indicate that if the plants are brought under cultivation the first plantations should be located in these interior districts, some of the most promising of which are those indicated above. Zonal position should be taken into account since it seems unlikely that the best sorts of Rabbit-brush can be grown to advantage outside of the Upper Sonoran Life Zone.

XV. SUMMARY

(1) It was the object of this investigation to discover a supply of rubber in native North American shrubs which might be used in time of war, thus rendering the nation to some extent independent of overseas importations of this substance. The studies were extended to include a preliminary inquiry into the possibility of bringing the plants under cultivation. *Chrysothamnus* or Rabbit-brush, was the genus of shrubs especially studied.

(2) The work was fostered by the Committee on Scientific Research of the State Council of Defense for California and by the University of California. It was furthered through the aid of a considerable number of correspondents.

(3) Chrysil is the name adopted for the particular kind of rubber found in *Chrysothamnus nauseosus*. It is a rubber of high grade and vulcanizes without difficulty.

(4) Rubber was found in two closely related genera of shrubs, namely, *Chrysothamnus* and *Haplopappus*. Only the former yields

Chrysil. The most important species of *Chrysothamnus* is *C. nauseosus*, under which are recognized twenty-two varieties. Twelve of these varieties have been examined and rubber found in all of them although individual plants may be devoid of rubber.

(5) *Chrysothamnus nauseosus* is a large shrub, the average weight being from four to six pounds. It grows readily from seed and reaches maturity in from six to eight years.

(6) The species is widely distributed in western North America, often inhabiting alkaline flats.

(7) The largest stands of Chrysil-bearing shrub are in Colorado, Nevada, and Utah. The plants with the highest rubber content are from Nevada and California. The total amount of rubber present in wild shrub is estimated at over 300,000,000 pounds.

(8) The rubber occurs in the individual cells, and is not a latex-rubber. Its place of occurrence in the plant has been rather definitely located. Methods have been developed for its detection by microscopical examination as well as by chemical analysis. Various experiments indicate that the chemical methods adopted are reasonably accurate; that great care must be exercised in the preparation of samples for analysis; and that samples do not deteriorate when stored for periods of several months.

(9) The results of one hundred and eighty chemical analyses and eighty microscopical examinations are tabulated. These indicate an average of 2.83 per cent of rubber in the variety *hololeucus*, 2.69 per cent in the variety *pinifolius*, 2.52 per cent in the variety *viridulus*, 1.97 per cent in the variety *consimilis*, and lower percentages in other varieties. The low-percentage varieties are all comparatively uncommon. The highest absolute percentage was found in a plant of *consimilis* collected near Gerlach, Nevada, which analyzed 6.57 per cent of pure rubber. The second-highest was a plant of *viridulus* from Benton, California, which yielded 5.56 per cent.

(10) Chrysil occurs in the plant in greatest amount at about the soil line. In the root it is present in only the upper part. In young twigs and leaves it occurs in only small amounts. The richest tissues are found in the cortex and the medullary rays, the former carrying much more than the latter.

(11) The amount of rubber varies with the botanical variety; the best varieties being those which inhabit alkaline soils.

(12) In harvesting wild shrub the whole plant should be taken, including four inches of root. Bulk may be reduced by removing the twigs. Cultivated plants might be so cut as to leave the base of the stem for regeneration.

(13) Because of the desirability of establishing the rubber-growing industry in the United States on waste lands *Chrysothamnus* and other plants should be further investigated with a view to making their cultivation a financial success.

(14) Its cultural requirements are such that *Chrysothamnus* could be grown on many of the alkaline plains of the West without irrigation; certain varieties endure winter temperature of —20° F.; others would withstand summer temperatures obtaining anywhere in the western states except possibly in the hottest valleys.

PLATE 18

Fig. 1. Photomicrograph of a portion of a cross-section of a twig of the current year—*viridulus*. Stained films in a few cells of the pith, absence of rubber in rays and in cortical parenchyma, accumulation of rubber in the bud intrusion. The chlorenchyma is heavily stained.

Fig. 2. Photograph of a portion of a cross-section of a five-year-old stem—*viridulus*.

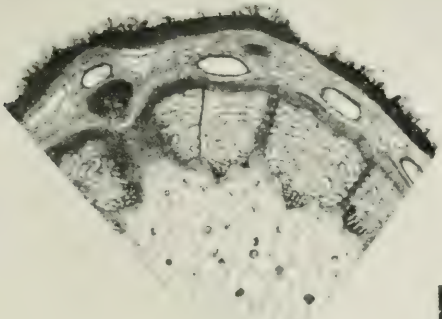
a. The outer limits of the rubber-bearing cortex.

b. The tangential zone of maximum, cortical, rubber deposition.

Fig. 3. Photograph of a portion of a three-year-old shoot—*viridulus*. No rubber in the pith.

c. The outer limits of the rubbear-bearing cortex.

Figs. 4 and 5. Photomicrographs showing nature of occurrence of rubber in the cell—*gnaphalodes*.



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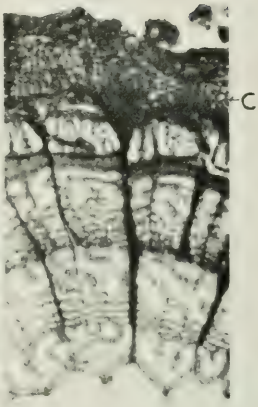

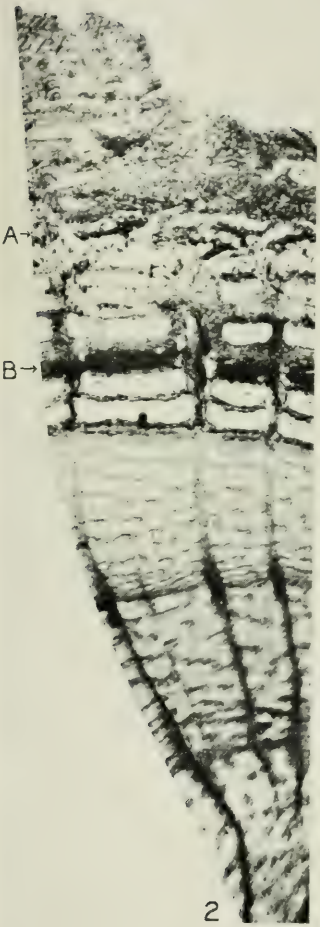

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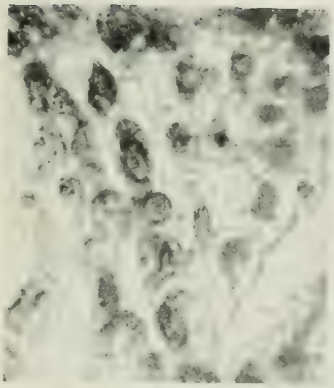

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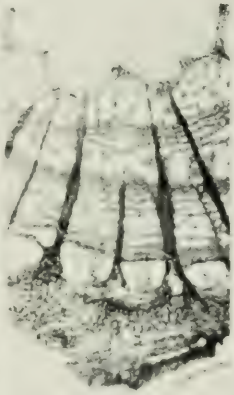

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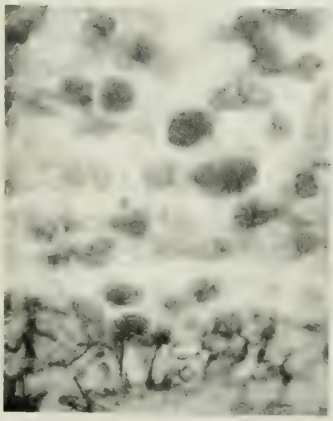

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PLATE 19

Fig. 1. Photomicrograph of a portion of a cross-section of a six-year-old stem—*speciosus*—showing the accumulation of rubber in the rays and their wide cortical extensions.

Fig. 2. Photograph of a portion of a particularly thin cross-section of a nine-year-old stem—*viridulus*.

a. The outer limits of the significant rubber-bearing cortex.

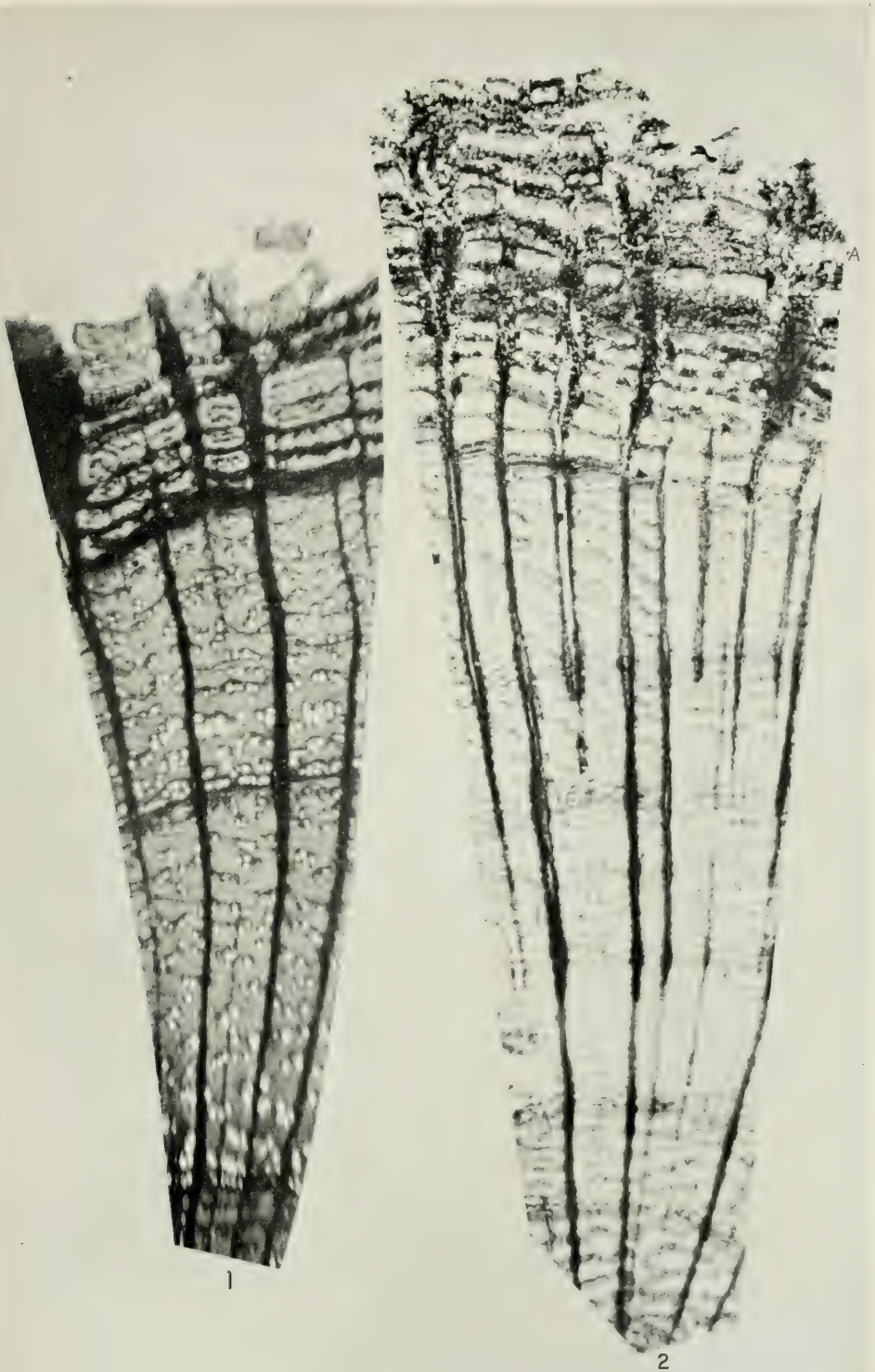
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PLATE 20

Chrysothamnus nauseosus var. *viridulus*. Plant H 3. To illustrate method for increasing weight of rubber-bearing parts.

Fig. 1. The wild plant as it appeared February 16, 1918. Height 5½ feet, spread 5 feet.

Fig. 2. The same plant after pruning, February 16, 1918. Greatest height 3½ feet. The cut branches are 276 in number, one to three years old, and average one-half inch thick.

Fig. 3. The same plant September 16, 1918. Height 4 feet 3 inches, spread 4 feet 6 inches. The number of branches has increased to 640. This increase is somewhat greater than in other plants subjected to the same treatment.

The black stake in figs. 1 and 2 is 40 cm. high. The short stake in all three figures is 4 inches high.

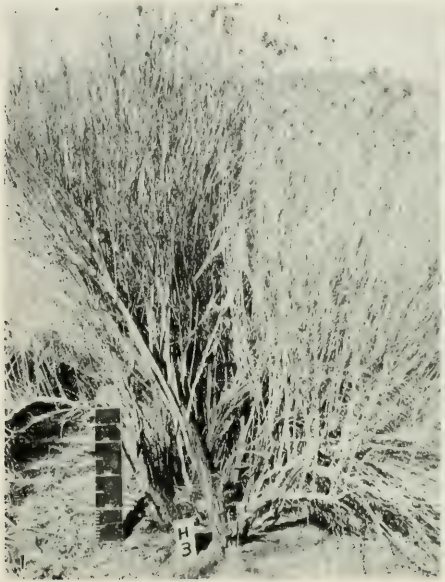

Fig. 1

Fig. 2

Fig. 3

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III. THE OCCURRENCE OF RUBBER IN CERTAIN WEST AMERICAN SHRUBS

BY

HARVEY MONROE HALL and THOMAS HARPER GOODSPEED

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I. *CHRYSOTHAMNUS* (EXCLUSIVE OF *C. NAUSEOSUS*) AND *HAPLOPAPPUS*

In a foregoing report attention has been paid almost exclusively to rubber as it occurs in the numerous varieties of *Chrysothamnus nauseosus*. In the course of the investigation we have also examined as many of the botanically related species and genera as were readily obtainable as well as some species of shrubs not closely related to *Chrysothamnus*. The total number of species of woody plants examined is seventy-nine. As a result of these examinations rubber is now known to occur in four other species of *Chrysothamnus* and in ten species of *Haplopappus*. In no case, however, were we able to detect rubber in any plant other than those showing a close botanical affinity to *Chrysothamnus*. Those in which rubber was found are indicated below. In the tables the percentage of pure rubber is indicated by the benzene extract. All percentages are based upon dry shrub except where "x" indicates that no moisture determination was made.

Chrysothamnus turbinatus (M. E. Jones) Rydb.

The general habit and appearance of this species is very much like that of certain varieties of *C. nauseosus*. Although it differs from that species in what appear to be important technical characters, such as the elongated, columnar involucre, it is not unlikely that further

study will reduce it to a variety of *nauseosus*. The plants are two to four feet high, round-topped, and very twiggy. They grow on sandy mounds of strongly alkaline clay flats. The species has been found only in Utah, and even there it is quite rare. A single sample (410) from the alkaline flats just east of Lund analyzed 4.88 per cent of rubber. Since the species is so close to *nauseosus* botanically it is probable that its rubber is also similar and should be referred to as Chrysil.

Fig. 1. *Chrysothamnus teretifolius* growing among the rocks at Benton Hot Springs, California. Plants average $1\frac{1}{2}$ feet high.

Chrysothamnus teretifolius (Dur. and Hilg.) Hall.

This is a low, broadly branched, woody plant, sometimes as much as six feet high and fully as broad, but usually much smaller (cf. fig. 1). Average plants will weigh one to three pounds. The largest we have seen had several trunks each eight inches thick and the whole plant had an estimated weight of twenty pounds. Unlike the genuine species of *Chrysothamnus* this one has a very resinous herbage and because of this it is placed in the genus *Ericameria* by some botanists. It grows on gravelly or stony hillsides, often in rocky cañon bottoms,

and although it never forms pure stands of any great extent yet a considerable supply could be assembled from some of the desert ranges. The distribution of *teretifolius* is from the easterly slope of the Sierra Nevada and Tehachapi mountains to central Nevada and possibly Arizona. The largest stands we have seen are in the cañons on both slopes of the White and Inyo ranges in eastern California; there is also a considerable quantity on the mountains to the west of Antelope Valley, California.

Table 1—Chemical Analyses

	Place of Collection	Date of Collection	Acetone Extract Per cent.	Benzene Extract Per cent.
45	Near Rosamond, Calif.	Oct. 26, 1917	5.46	2.80
436	Lida, Nev.	Sept. 10, 1918	2.85	1.67
440	West of Deep Spring Valley, Calif.	Sept. 12, 1918	2.22	2.48
575	Near Benton, Calif.	Dec. 23, 1918	4.61	4.51[x]
592	Near Victorville, Calif.	Dec. 25, 1918	4.93	2.04[x]

Microscopical Examinations

	Place of Collection	Date of Collection	Estimated Amount
61	Near Bishop, Calif.	Nov. 1, 1917	Fair
67	Benton Hills, Calif.	Nov. 4, 1917	Fair
76	Near Candelaria, Nev.	Oct. 8, 1917	Poor
82	Near Benton, Calif.	Nov. 11, 1917	Good
83	Silver Cañon, Inyo Mts., Calif.	Nov. 12, 1917	Fair
85	Near Owenyo, Inyo Co., Calif.	Nov. 14, 1917	Fair

Chrysothamnus paniculatus (Gray) Hall.

The plants of this species are on the average taller and less spreading than *C. teretifolius* but they have a similarly glandular-dotted foliage and the two are very close botanically. It grows on the southerly part of the Mojave Desert and from Whitewater, on the west side of the Colorado Desert, east to Arizona but it is nowhere abundant. Six samples have been examined, with the following results.

Table 2—Chemical Analyses

	Place of Collection	Date of Collection	Acetone Extract Per cent.	Benzene Extract Per cent.
579	North of Barstow, Calif.	Dec. 24, 1918	2.73	1.20[x]
580	North of Barstow, Calif.	Dec. 24, 1918	4.10	3.24[x]

Microscopical Examinations

	Place of Collection	Date of Collection	Estimated Amount
96	Cabazon, Calif.	Jan. 22, 1918	Fair
98	West of Whitewater, Calif.	Jan. 22, 1918	Fair
99	North side of San Jacinto Mountain, Calif.	Jan. 22, 1918	Fair
581	North of Barstow, Calif.	Dec. 24, 1918	Poor

Chrysothamnus linifolius Greene.

This is perhaps only a variety of *C. viscidiflorus* but it differs from all other forms of that exceedingly variable species in the taller and more robust habit (the woody stems are sometimes eight feet high), in the broadly linear leaves, and in the greenish thickened tips of the involucral bracts. Its ecologic habitat is also different, since it grows only in alkaline soil, whereas the forms of *viscidiflorus* are confined to well drained, non-alkaline slopes and benches. This may account for the occurrence of rubber in *linifolius*, and its absence in *viscidiflorus* as well as in two other very closely related upland species, namely, *humilis* and *puberulus*. This is in accord with what has been found in *C. nauseosus*, in which species, as noted elsewhere,[1] the varieties carrying the most rubber are all inhabitants of alkaline soils.

Only two samples of *linifolius* have been examined. One (400) from an alkaline flat near Grand Junction, Colorado, yielded on analysis 1 per cent of rubber. The other (515), which was gathered at Green River, Utah, was not analyzed. A microscopic examination failed to detect any rubber in it.

Haplopappus nanus D. C. Eaton

The stems of this species are very low, one foot or less in height, much gnarled and branched and with numerous short leafy twigs. They have a thick, corky bark and a considerable portion of the wood is dead in many of the plants. The foliage is deep green and quite resinous. Average plants will weigh about one pound but it is usually impossible to obtain the whole plant since the roots are tightly held by the rocks in which they grow. The species inhabits rocky ledges and outcroppings and may be expected on almost any of the mountain ranges of the Great Basin area. It is known to grow in such situations from Mono County, California, to southwestern Utah and north to Washington. Wherever we have found it during the course of these investigations it was growing in only limited quantities and there are probably no considerable stands of it anywhere. (See fig. 2.)

The percentage of rubber in *Haplopappus nanus* is the highest known for any native American shrub except Guayule, our analyses, four in number, indicating that it runs from 6 to 10 per cent of the dry weight of the entire plant. The quality of the product would probably be inferior to that of the *viridulus* form of *Chrysothamnus* because of the large amount of resins present. A sample was worked out mechan-

[1]See p. 245.

ically, separated in water, and found to be rather soft and dark colored. It was not subjected to detailed examination. The recovery of any considerable amount of rubber from the wild shrub is practically impossible because of the very limited known supply. It is conceivable that under cultivation it might grow to good size and at the same time retain its fairly high rubber content and that both the size of plant and percentage of rubber could then be increased by selection or breeding, but the outlook for this is not promising.

Six samples have been examined and five of them are reported on below. A considerable variation in the rubber content is to be expected since much depends upon the amount of dead wood present in the sample. Usually this is considerable since the plants are very old and grow under extremely adverse conditions. The analyses are for the whole plant (after the obviously dead branches had been removed) except that only the upper portion of the root is included. One other sample (438, from near Deep Spring Valley, California) was analyzed with the result that the amount of the benzene extract was negligible. This is omitted from the table since the plant was not in a condition to permit of a positive identification. It may belong to some other species or even to another genus.

Fig. 2. *Haplopappus nanus*, plant no. 206, Benton Hills, California. Total height as illustrated, 1½ feet.

TABLE 3.—CHEMICAL ANALYSES

	Place of Collection	Date of Collection	Acetone Extract Per cent.	Benzene Extract Per cent.
71	Near Benton, Calif.	Nov. 4, 1917	7.85*	9.46*
206	Near Benton, Calif.	Feb. 19, 1918	9.57	6.72
256	Shoshone Falls, Idaho	June 23, 1918	5.86	4.61
416	Caliente, Nev.	Sept. 6, 1918	4.49	8.42

MICROSCOPICAL EXAMINATION

	Collection	Date of Collection	Estimated Amount
75	Near Candelaria, Nev.	Oct. 8, 1917	Good

*Based on air-dried sample analyzed by Professor P. L. Hibbard; if perfectly dry the benzene extract would probably be between 9.6 and 10 per cent.

Haplopappus cervinus Wats.

This is a low shrub, scarcely a foot high, with resinous-punctate leaves. It grows in the foothill cañons of western Utah and is especially common along the east side of Salt Lake Valley, where, however, it does not grow in continuous belts. The quality of the rubber is probably similar to that of *Haplopappus nanus*, of which *cervinus* is perhaps only a variety. The above-ground portions of four samples submitted by Professor Marcus E. Jones have been analyzed with the following result.

Table 4—Chemical Analyses

	Place of Collection	Date of Collection	Acetone Extract Per cent.	Benzene Extract Per cent.
510	Near Salt Lake, Utah	Oct. 7, 1918	4.63	4.03
535	Parleys Cañon, Utah	Dec. 22, 1918	5.58	2.28
536a	Parleys Cañon, Utah	Dec. 22, 1918	5.68	2.21
537	Parleys Cañon, Utah	Dec. 22, 1918	5.54	2.90[x]

Haplopappus ericoides (Less.) H. & A.

This heather-like shrub grows one to five feet high. The main stems are one to three inches thick at base, either erect or decumbent, and emit numerous erect branchlets densely clothed with short narrow leaves, the whole plant thus resembling heather. The herbage is green and resinous. The plants grow in sandy soil and are most abundant as well as of greatest size in the sand dunes along the seashore, where they sometimes form extensive colonies. The species extends geographically along the California coast from southern Los Angeles County to San Francisco. The distribution of rubber in this plant is peculiar, if a sample gathered in the sand dunes near Moss Beach, south of San Francisco, is characteristic of the species. Only traces of rubber were found in the stems of this plant but in the root, which was analyzed in sections, the percentage gradually increased until at a depth of two feet it was 3.92.

TABLE 5—CHEMICAL ANALYSES

	Place of Collection	Date of Collection	Acetone Extract Per cent.	Benzene Extract Per cent.	Remarks
93	Duarte, Calif.	Jan. 20, 1918	5.49	0.49	Base of stem
149	Moss Beach, Calif.	May 23, 1918	9.17	3.92	End of root; 50 cm. below soil line
	Moss Beach, Calif.	May 23, 1918	7.47	3.11	Next 20 cm. up root
	Moss Beach, Calif.	May 23, 1918	5.16	1.67	Next 20 cm. up root
	Moss Beach, Calif.	May 23, 1918	5.49	0.58	10 cm. below soil line
157	San Francisco, Calif.	July 27, 1918	6.67	2.10	Root; piece 50 cm. below soil line
	San Francisco, Calif.	July 27, 1918	5.14	0.75	Root; piece 10 cm. below soil line
	San Francisco, Calif.	July 27, 1918	9.10	0.19	Base of stem
743	Duarte, Calif.	Jan. 1, 1919	3.72	0.13	Base of stem
	Duarte, Calif.	Jan. 1, 1919	7.51	0.25	Twigs
	Duarte, Calif.	Jan. 1, 1919	3.95	0.90	Entire root
744	Duarte, Calif.	Jan. 1, 1919	3.11	0.27	Stem
745	Duarte, Calif.	Jan. 1, 1919	4.07	0.38	Stem
	Duarte, Calif.	Jan. 1, 1919	4.81	1.97	Root
	Duarte, Calif.	Jan. 1, 1919	3.32	0.19	Tops; 3 years old and younger

MICROSCOPICAL EXAMINATIONS

	Place of Collection	Date of Collection	Estimated Amount
95	Claremont, Calif.	Jan. 20, 1918	Poor
137	San Francisco, Calif.	Mar. 28, 1918	Poor
138	San Francisco, Calif.	Mar. 28, 1918	Poor
156	San Francisco, Calif.	July 27, 1918	Poor

Haplopappus Palmeri Gray.

In habit and general appearance this species is much like *H. cricoides* except that the plants are usually smaller. It belongs to southern California and is especially common on the plains and lower foothills of the coastal slopes. It is absent from the sand dunes along the coast. One sample (725) from Riverside was found to contain 0.91 per cent of rubber. Another (721), also from Riverside, and one (201) from Colton were examined microscopically but no rubber could be detected in either of them.

Haplopappus pinifolius Gray.

This southern California species is much like *H. ericoides*. One collection (129) made near San Bernardino, was examined microscopically, and found to contain but a small amount of rubber. A second sample was taken in San Fernando Valley and found to contain 1.61 per cent in the basal portion of the stem.

Haplopappus monactis Gray.

This is a good sized shrub, commonly two or three feet high, sometimes six feet high and with a trunk diameter of four inches; in one case there were three principal branches, each one to three inches thick. The weight is estimated at five pounds for average plants; thirty pounds for exceptionally large ones. The species is most abundant around the westerly extensions of the Mojave Desert but it grows at many places along the desert borders and east into southern Nevada; also to a very limited extent on the coastal slope of southern California. One large shrub (90) was collected near Elizabeth Lake and examined microscopically. It appeared to contain a fair amount of rubber. A much smaller one (713) from near Hesperia was analyzed and found to contain only 0.38 per cent of rubber.

Haplopappus laricifolius Gray.

Very close botanically to *H. monactis*, this species is also like it in habit, general appearance, and rubber content. It grows in southern Arizona, but apparently it is not abundant. Five samples have been examined with the result indicated below.

Table 6—Chemical Analyses

	Place of Collection	Date of Collection	Acetone Extract Per cent.	Benzene Extract Per cent.
760	Near Tucson, Ariz.	Feb. 18, 1919	3.44	5.16
783*	Santa Catalina Mts., Ariz.	Mar. 16, 1919	5.44	2.32
783†	Santa Catalina Mts., Ariz.	Mar. 16, 1919	3.62	3.37
786*	Tucson Mts., Ariz.	Mar. 23, 1919	3.94	2.01
786†	Tucson Mts., Ariz.	Mar. 23, 1919	3.33	2.87

* Stem.
† Root.

Microscopical Examination

	Place of Collection	Date of Collection	Estimated Amount
158	Near Tucson, Ariz.	July 27, 1918	Fair

Haplopappus arborescens (Gray)[2]

Although this is one of the largest species of the genus it is not really arborescent, as its specific name would seem to indicate. However, the woody stems are often several inches thick at the base and the shrubs are commonly three to five feet high. The species is common in the Coast Ranges of middle California and occurs also in the foothills of the Sierra Nevada. Two specimens (151, 152), both from one station on Mt. Tamalpais, showed only traces of rubber on microscopical examination.

Haplopappus brachylepis (Gray)[3]

The geographic distribution of *H. brachylepis* is restricted to a small area in southwestern San Diego County, California, and to northern Lower California. The species is a large shrub, commonly three to six feet high, with brittle stems. It grows in the arid chaparral belt, usually on stony hillsides. Four samples taken in San Diego County, near the borders of Lower California, were examined with results as indicated below.

TABLE 7—CHEMICAL ANALYSES

	Place of Collection	Date of Collection	Acetone Extract Per cent.	Benzene Extract Per cent.
728	El Campo, Calif.	Dec. 29, 1918	13.18	0.81
730	El Campo, Calif.	Dec. 29, 1918	10.69	0.16

MICROSCOPICAL EXAMINATIONS

	Place of Collection	Date of Collection	Estimated Amount
727	El Campo, Calif.	Dec. 27, 1918	Nothing
729	El Campo, Calif.	Dec. 29, 1918	Traces

Haplopappus linearifolius DC.

This is an erect shrub two to five feet high, with stems commonly one to four inches thick, and resinous herbage. It grows from Lake County, in the Coast ranges, south into Lower California and east to southern Utah and Arizona. It is perhaps most plentiful around the borders of Antelope Valley, California. There are two forms. Typical *linearifolius* grows in the Coast ranges. The other form, distinguished by its shorter leaves and smaller heads, replaces it in the desert country and is known as var. *interior* (Coville) M. E. Jones.

[2] *Haplopappus arborescens* (Gray) H. M. Hall, comb. nov. *Linosyris arborescens* Gray, Bot. Mex. Bound. (1859), p. 79.

[3] *Haplopappus brachylepis* (Gray) H. M. Hall, comb. nov. *Bigelovia brachylepis* Gray, Bot. Calif., vol. 1 (1876), p. 614.

In the following tabulation of examinations, only nos. 492 and 493 represent typical *linearifolius;* the remainder are of the *interior* variety.

Table 8. Chemical Analyses

	Place of Collection	Date of Collection	Acetone Extract Per cent.	Benzene Extract Per cent.
492	South of Antioch, Calif.	Oct. 12, 1918	2.47	0.30
493	South of Antioch, Calif.	Oct. 12, 1918	1.53	0.03
701	Mojave Desert, Calif.	Dec. 25, 1918	3.15	1.21
702	Mojave Desert, Calif.	Dec. 25, 1918	3.32	1.32
703	Mojave Desert, Calif.	Dec. 25, 1918	3.13	1.19
714	Near Hesperia, Calif.	Dec. 26, 1918	2.78	0.45

Microscopical Examination

	Place of Collection	Date of Collection	Estimated Amount
89	Del Sur, Antelope Valley, Calif.	Jan. 19, 1918	Poor

II. REGIONAL DISTRIBUTION OF RUBBER IN *HAPLOPAPPUS*

We have shown that Chrysil is peculiar to the part of the plant above ground, analyses of root and stem indicating that below a point approximately 10 cm. beneath the soil line rubber occurs in negligible quantities even if the parts above are relatively rich in this substance. In the case of at least two species of *Haplopappus* a different distribution obtains as is indicated by the results given in the following table.

TABLE 9—REGIONAL DISTRIBUTION OF RUBBER IN *Haplopappus*

Collection Number	Species	Place of Collection	Date of Collection	Acetone Extract Per cent.	Benzene Extract Per cent.	Remarks
149	Haplopappus ericoides	Moss Beach, Calif.	May 23, 1918	9.17	3.92	End of root 50 cm. below soil line
		Moss Beach, Calif.	May 23, 1918	7.47	3.11	Next 20 cm. up root
		Moss Beach, Calif.	May 23, 1918	5.16	1.67	Next 20 cm. up root.
		Moss Beach, Calif.	May 23, 1918	5.49	0.58	10 cm. below soil line
157	Haplopappus ericoides	San Francisco, Calif.	July 27, 1918	6.67	2.10	Root; piece 50 cm. below soil line
		San Francisco, Calif.	July 27, 1918	5.14	0.75	Root; piece 10 cm. below soil line
		San Francisco, Calif.	July 27, 1918	9.10	0.19	Base of stem
206	Haplopappus nanus	Near Benton, Calif.	Feb. 19, 1918	9.57	6.72	Stem
		Near Benton, Calif.	Feb. 19, 1918	5.96	5.29	Root
256	Haplopappus nanus	Shoshone Falls, Idaho	June 23, 1918	22.58	0.64	Leaves
		Shoshone Falls, Idaho	June 23, 1918	8.94	2.69	Twigs
		Shoshone Falls, Idaho	June 23, 1918	5.86	4.61	Stem
743	Haplopappus ericoides	Duarte, Calif.	Jan. 1, 1919	3.72	0.13	Base of stem
		Duarte, Calif.	Jan. 1, 1919	7.51	0.25	Twigs
		Duarte, Calif.	Jan. 1, 1919	3.95	0.90	Entire root
745	Haplopappus ericoides	Duarte, Calif.	Jan. 1, 1919	4.07	0.38	Stem
		Duarte, Calif.	Jan. 1, 1919	4.81	1.97	Root
		Duarte, Calif.	Jan. 1, 1919	3.32	0.19	Tops; 3 years old and younger

It seems clear from the results included in the above table that the root areas of the two species of *Haplopappus* examined contain appreciable quantities of rubber. In the case of *H. ericoides* the parts above the soil line are strikingly deficient in rubber as compared with the roots. Indeed, in the extremities of the root the percentage is often highest and decreases as one passes upward towards the soil line. The regional distribution in *ericoides* is, thus, the reverse of that found in the various varieties of *Chrysothamnus*.

In *H. nanus*, on the other hand, stem and root appear to bear equal quantities of rubber. The evidence here is obviously fragmentary but the above statement holds rather strictly for 206, and in the case of 256 the stem probably bears a maximum quantity for this plant and it might be assumed that the root, if analyzed, would show an approximately equal amount.

It appears, then, that three types of regional distribution of contained rubber are shown by the plants which we have examined in the course of the entire investigation. In the first place, the maximum quantity is borne by the stem. This is peculiar to the distribution of Chrysil. In the second place, root and stem bear equal amounts. This condition obtains in *Haplopappus nanus*. Finally, we have the case in which the root carries almost the entire amount of rubber borne by the plant, *H. ericoides*. This seems a rather remarkable situation and one which would repay further investigation. In particular it would be important to examine in detail the distribution of rubber in the other species of *Haplopappus* not investigated in this particular connection by us.

III. SPECIES IN WHICH NO RUBBER WAS FOUND

In the course of the investigation reported on in the foregoing pages a miscellaneous collection of plants was made as opportunity offered and these have been examined histologically for rubber content with the result that rubber was located in certain cases but only in species of *Chrysothamnus* or of related genera. This occurrence has been noted in the preceding list but it now remains to enumerate those species in which no rubber could be detected with certainty. This list is given as it may be of some service in case a more extensive survey is undertaken. As in the preceding report, the numbers refer to field notes and have been assigned merely for convenience of reference. The locality mentioned in each case is the place of collection.

I. COMPOSITAE

700. *Acamptopappus sphaerocephalus.* Near Hesperia, California.
491. *Artemisia californica.* Antioch, California.
19. *Artemisia filifolia.* Denver, Colorado.
460. *Artemisia Rothrockii.* Tioga Pass, California.
8. *Artemisia tridentata.* Truckee, California.
589. *Baccharis glutinosa.* Barstow, California.
747. *Baccharis pilularis.* Near Ventura, California.
97. *Baccharis sergiloides.* Near Banning, California.
751. *Bebbia juncea.* Palm Springs, California.
595. *Brickellia atractyloides.* Near Victorville, California.
596. *Brickellia desertorum.* Near Victorville, California.
513*a*. *Brickellia microphylla.* Near Salt Lake, Utah.
409. *Chrysothamnus Greenei.* Lund, Utah.
285. *Chrysothamnus Howardi.* Near Walsenburg; also no. 287, Cañon City, and no. 292, Villa Grove; all in Colorado.
458. *Chrysothamnus nevadensis.* Mono Mills, California.
18. *Chrysothamnus Parryi.* Teller Lake, Colorado.
9. *Chrysothamnus humilis.* Truckee Valley, California.
14. *Chrysothamnus puberulus.* Pyramid Lake, Nevada; also 23, Tonopah, Nevada; also 28, 29, Reno, Nevada; and 259, southeastern Idaho.
7. *Chrysothamnus viscidiflorus* var. *tortifolius.* Truckee Valley, California; also 30, Reno, Nevada.
746. *Corethrogyne filaginifolia.* Near Ventura, California.
763. *Dysodia porophylloides.* Palm Springs, California.
736. *Encelia californica.* Near San Diego, California.
598. *Encelia farinosa.* Near Victorville, California; also 722, Riverside, California.
68. *Ericameria cuneata spatulata.* Benton, Mono County, California; also near Victorville, California.
86. *Franseria dumosa.* Owenyo, California; also 587, Barstow, California.
594. *Gnaphalium bicolor.* Near Victorville, California.
490. *Gutierrezia californica.* Antioch, California.
46. *Guiterrezia lucida.* Rosamond, California; also 586, Barstow, California.
558. *Gutierrezia Sarothrae.* Near Reno, Nevada.
38. *Haplopappus Bloomeri.* Truckee, California.
273. *Haplopappus Fremonti.* Laramie, Wyoming.
735. *Hazardia squarrosa.* El Campo, San Diego County, California.
764. *Hofmeisteria pluriseta.* Palm Springs, California.
73. *Hymenoclea salsola.* Mina, Nevada; also 585, Barstow, California.
761. *Isocoma coronopifolia.* Near Tucson, Arizona.
160. *Isocoma Hartwegi.* Near Tucson, Arizona; also 762, from Tucson.
427. *Isocoma veneta acradenia.* Las Vegas, Nevada; also 599, Victorville, California.
94. *Lepidospartum squamatum.* Duarte, California.
242. *Picradenia Lemmoni.* Near Weed, California.
560. *Tetradymia canescens.* Near Reno, Nevada; also 433, Goldfield, Nevada.

II. MISCELLANEOUS FAMILIES

711. *Astragalus leucopsis* (*Leguminosae*). Near San Diego, California.
425. *Atriplex canescens* (*Chenopodiaceae*). Las Vegas, Nevada.
24. *Atriplex confertifolia* (*Chenopodiaceae*). Tonopah, Nevada; also 582, Barstow, California.
740. *Cneoridium dumosum* (*Rutaceae*). Near San Diego, California.
31. *Ephedra nevadensis* (*Gnetaceae*). Reno, Nevada
707. *Eriodictyon californicum* (*Hydrophyllaceae*). Mojave Desert, California.
432. *Eriogonum fasciculatum* var. (*Polygonaceae*). Goldfield, Nevada.
494. *Eriogonum nudum* (*Polygonaceae*). Mt. Diablo, California.
74. *Eurotia lanata* (*Chenopodiaceae*). Mina, Nevada.
734. *Frasera Parryi* (*Gentianaceae*). El Campo, San Diego County, California.
426. *Glycyrrhiza lepidota* (*Leguminosae*). Las Vegas, Nevada.
597. *Isomeris arborea* (*Capparidaceae*). Near Victorville, California.
584. *Larrea divaricata* (*Zygophyllaceae*). Near Barstow, California.
429. *Lepidium Fremonti* (*Cruciferae*). Indian Spring, Nevada.
583. *Lycium Cooperi* (*Solanaceae*). Near Barstow, California.
422. *Olneya tesota* (*Leguminosae*). Las Vegas, Nevada.
423. *Prosopis juliflora* (*Leguminosae*). Las Vegas, Nevada.
424. *Prosopis pubescens* (*Leguminosae*). Las Vegas, Nevada.
742. *Rhamnus crocea* (*Rhamnaceae*). Near San Diego, California.
739. *Rhus integrifolia* (*Anacardiaceae*). Near San Diego, California.
732. *Rhus ovata* (*Rhamnaceae*). El Campo, San Diego County, California.
420. *Rhus trilobata* (*Anacardiaceae*). Las Vegas, Nevada; also 733, El Campo, California.
15. *Sarcobatus vermiculatus* (*Chenopodiaceae*). Near Pyramid Lake, Nevada; also 33, same locality.
738. *Simmondsia californica* (*Buxaceae*). Near San Diego, California.

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PHYCOLOGICAL CONTRIBUTIONS
I

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BY

WILLIAM ALBERT SETCHELL AND NATHANIEL LYON GARDNER

Hormiscia doliifera sp. nov.

Filamentis 3–4 cm. longis, dum juvenis prope cylindicis, ad basim tantummodo attenuatis, rhizoideis extramatricalibus e segmentis paucis infernis oriundis adjunctis, atroviridibus; segmentis fertilibus 80–130μ usque ad 184μ diam., 0.75–1.25-plo diam., longioribus, doliiformibus, parietibus tenuibus, 5–7μ crassis, hyalinis, homogeneis; chromatophoris tenuibus fenestratis taeniaeformibus, parietalibus, pyrenoideis parvis numerosis.

Filaments 3–4 cm. long, nearly cylindrical throughout when young, tapering only at the base, attached by extramatrical rhizoids from a few of the lower segments; color dark green; fertile segments 80–130μ, up to 184μ diam., 0.75–1.25 times as long, doliiform, with thin, 5–7μ thick, hyaline, homogeneous walls; chromatophore a thin fenestrate parietal band, with numerous small pyrenoids.

Growing on rocks in the upper littoral belt. South side of the Golden Gate, San Francisco, California. July, 1918. Type no. 4462, Gardner.

Hormiscia doliifera resembles most closely *Urospora Hartzii* Rosenvinge (1893, p. 922) and *U. incrassata* Kjellman (1897, p. 7). From each of these species it differs in having filaments of larger diameter, in having more uniformly swollen, sometimes almost spherical, fertile segments, and in having the segments more nearly uniform in length, averaging a little less than quadrate. From *U. incrassata* it differs also in its strictly extramatrical rhizoids. It approaches also the little known *U. crassa* Rosenv., but its segments seem never so short as represented for that species. It is much too slender for *Hormiscia collabens* (i.e., up to 450μ), as indicated by Batters (1894, p. 114). The filaments are decidedly larger than any dimensions given for

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H. penicilliformis (Roth) Fries and the chromatophore is thinner, usually more coarsely reticulate, and with many more and much smaller pyrenoids.

Spongomorpha Mertensii (Rupr.) comb. nov.

Conferva Mertensii Ruprecht, Tange, 1851, p. 403.
Conferva viminea Ruprecht, *loc. cit.* (fide Yendo, 1916, p. 246).
Cladophora Mertensii De-Toni, Syll. Alg., vol. 1, 1889, p. 317.
Cladophora viminea De-Toni, *loc. cit.*, p. 318.
Spongomorpha arcta var. *limitanea* Collins, Green Alg. N. A., Suppl. I, 1912, p. 97, *in* Collins, Holden and Setchell, Phyc. Bor.-Amer. (Exsicc.), no. 1736.
Acrosiphonia Mertensii (Rupr.) Yendo, Notes on algae new to Japan V, 1916, p. 246.

It seems best to follow Yendo (*loc. cit.*) in considering the *Conferva Mertensii* Rupr. distinct, and we refer here, for the present at least, the *Spongomorpha arcta* var. *limitanea* Collins. The species, as we understand it, has no spiny branches or branchlets, but usually shows circinate, simple or compound, branchlets. Since we prefer *Spongomorpha* to *Acrosiphonia*, we are compelled to establish the new combination given above.

Capsosiphon fulvescens (Ag.) comb. nov.

Ulva fulvescens Agardh, Sp. Alg., 1822, p. 420.
Ilea fulvescens J. Agardh, Till Alg. Syst., pt. 3, 1882, p. 115, pl. 4, figs. 95–99.
Ulva aureola Agardh, Icon. Alg. Eur., 1829, pl. 29.
Capsosiphon aureolum Gobi, Ber. Alg. Forsch. im Finn. Meerbus., 1877, etc., 1879, p. 88.

We feel compelled to accept the dictum of J. G. Agardh (*loc. cit.*) that the *Ulva fulvescens* of C. A. Agardh is only a younger condition of *Ulva aureola* C. A. Agardh. Since it seems to us, also, that the proper generic designation is *Capsosiphon*, the new combination proposed above is rendered necessary.

Enteromorpha groenlandica (J. Ag.) comb. nov.

Monostroma groenlandicum J. Agardh, Till Alg. Syst., pt. III, 1882, p. 107, pl. 3, figs. 80–83; Collins, Green Alg. N. A., 1909, p. 208; Saunders, Alg. Harriman Exp., 1901, p. 410; Setchell and Gardner, Alg. N. W. Amer., 1903, p. 208.

Enteromorpha groenlandica has always been puzzling as to its proper placing. While technically it may seem to belong to the genus *Monostroma*, under which it was originally described, more properly than to any other genus of the Ulvaceae, yet its slender filiform habit certainly more closely resembles that of some species of *Enteromorpha*. From *Enteromorpha*, however, it differs in not having its cells set sufficiently closely together to be parenchymatous in appearance. It is at first solid, becoming hollow only late, but never rupturing longitudinally and opening out into a membrane as do the characteristic species of *Monostroma*. Certain species of *Enteromorpha* show a tendency towards abundance of intercellular jelly at times, while certain species of *Monostroma* are parenchymatous. It seems best to us, therefore, to transfer this species to *Enteromorpha*.

Monostroma areolatum sp. nov.

Plate 30 and plate 31, figure 2

Thallo delicatissimo, lubrico, 20–35 cm. alto, sessili, juveno saccato, mox fisso et lobos late ovatos aut obovatos, undulatos, plicatos et crispatos formanti, dilute viridi; membrana distincte minuteque areolata, 9–12μ crassa; cellulis rotunde angulatis, 6–7μ crassis in sectione transversali subsphericis, in areolis quibusque aggregatis.

Frond very delicate, lubricous, 20–35 cm. high, sessile, saccate when young, soon splitting and forming numerous, long, broadly ovate, or obovate, undulate, plicate and crisped lobes, pale green; membrane distinctly and finely areolate, 9–12μ thick; cells with rounded angles, 6–7μ diam., subspherical in cross-section, grouped within each areole.

Growing on *Zostera* in quiet waters. Sitka, Alaska. Type no. 3924, Gardner.

This species of *Monostroma* is exceedingly beautiful and is among the most delicate and flaccid of the genus. The frond remains saccate for only a brief period, attaining a height of only a millimeter or two. The sack then breaks and the membrane spreads out at once, early developing small lobes. Finally a few primary lobes are established and these develop numerous secondary lobes. The growth on the whole margin greatly exceeds that of the interior, and this results in the production of a great number of folds, making the margin very much crisped. In the thickness of the frond and shape of the cells *M. areolatum* closely approximates *M. zostericola* Tilden. The cells of the latter are, however, more angular and more closely placed and the frond is not divided into areolae. There is a marked difference

in the size of these two species, as well as in their methods of development. *M. zostericola* is diminutive, remains saccate for some time, and splits longitudinally, forming several lobes broadening outward. *M. arcolatum* very closely resembles the genus *Prasiola* in the grouping of the cells as seen in surface view.

Ulva stenophylla sp. nov.

Plate 26, figure 2, and plate 29

Thallo simplici, lineari-lanceolato, ad basim in stipitem brevissimum, complanatum, cuneatum longe attenuato, 5–8 dm. longo, 5–10 cm. lato, medio plano, marginibus undulatis; membrana 60–110μ crasso, cellulis e superficie quadratis, 14–20μ diam. in sectione transversali, 1.5–2-plo diam. longioribus; chromatophoris tenuibus, parietalibus, omnino aut partim cellulam tegentibus; pyrenoidibus nullis.

Frond simple, linear-lanceolate, tapering abruptly at the base to a very short, flattened, cuneate stipe, 5–8 dm. high, 5–10 cm. wide, plane in the middle with undulate margins; membrane 60–110μ thick; cells squarish in surface view, 14–20μ diam., 1.5–2 times as long as the diameter in section, chromatophore a thin, parietal layer, covering a part or the whole of the cell; pyrenoids absent.

Growing on rocks in the lower littoral belt. Central California. Type no. 5445 (Herb. Univ. Calif., no. 98511), Setchell.

The plants described under this name are quite distinct from the other species of *Ulva*, in shape, in texture and in anatomical details. They are dark green, tough and harsh to the touch. The usually simple, long, lanceolate shape serves to distinguish them from other species at a glance.

Ulva vexata sp. nov.

Plate 22, figures 4–7

Thallo parvo, simplici, rigido, lineari ad oblanceolato aut spatulato, plano aut parce undulato, plus minusve bullato, basi cuneato stipite parvo et solido, 1–3 cm. longo, 3–10 mm. lato, atroviridi, siccitate atro; membrana 45–55μ usque ad 100μ crassa, cellulis verticaliter elongatis, 11–15μ usque ad 18μ longis, 3.5–5μ crassis, parietibus crassis et e superficie angulos obtusos ostendentibus; chromatophoris cellulas implentibus; pyrenoidibus nullis.

Frond small, unbranched, rigid, linear to oblanceolate or spatulate, plane or slightly undulate, more or less bullate with cuneate base and small, solid stipe, 1–3 cm. long, 3–10 mm. wide, dark green, black on drying; membrane 45–55μ, up to 100μ thick, cells vertically elongated, 11–15μ, up to 18μ long, 3.5–5μ wide, with thick walls and very blunt angles in surface view; chromatophore filling the cell, pyrenoids absent.

Growing on rocks along high-tide level. In the vicinity of San Francisco, California. Type no. 4444, Gardner.

Ulva californica Reed, Two ascomycetous fungi, etc., 1902, p. 149 (not of Wille).

Ulva vexata has been observed only in the vicinity of San Francisco, as mentioned above, where it grows in considerable profusion. It seems quite probable that it may be much more widely distributed both north and south of San Francisco. It might be suspected of being a malformation due to the parasite always found more or less infesting it, but the size and proportions of the cells of the less parasitized portions seem to mark it as a distinct species.

Ulva angusta sp. nov.

Plate 27 and plate 31, figure 1

Thallo simplici aut rarissime lobato, lanceolato aut oblanceolato, 8–15 cm. longo, 0.5–1.5 cm. lato, 35–45μ (interdum prope 53μ) crasso, basi aut longe abrupto ad stipitem delicatum solidumque attenuato, disco affixo, dilute viridi, marginibus fere planis usque ad crispatissimis; cellulis e superficie 3–6 lateralibus angulis rotundis, 5–12μ diam. sectione transversali quadratis ad 1.5-plo longioribus, angulis rotundis; chromatophoris dimidium externum cellularum implentibus; pyrenoidibus singulis.

Frond simple or very rarely lobed, lanceolate to oblanceolate, 8–15 cm. long, 0.5–1.5 cm. wide, 35–45μ thick (occasionally about 53μ), tapering either gradually or abruptly at the base to a delicate, solid stipe with discoid holdfast, color of fronds pale green, margins varying from almost plane to very much crisped; cells in surface view 3–6 sided, with rounded angles, 5–12μ diam. in section, quadrate to one and a half times longer than broad, with rounded angles; chromatophore filling the outer half of the cell; pyrenoid single.

Growing in shallow pools along high-tide level. Moss Beach, San Mateo County, California, April, 1919. Type no. 4430, Gardner.

We find at several places along the coast of central California a rather short and narrow *Ulva* which does not seem to belong to any of the hitherto described species. We have felt compelled, therefore, to give it a name. It resembles the *Phycoseris lapathifolia* of Kuetzing (1856, pl. 25), but is shorter and narrower. It also resembles, even more closely, Kuetzing's figure of *Phycoseris Linza* (1856, pl. 16, fig. 1), but is a smaller plant than that also. The short, flattened stipe is solid. The narrow blade varies from plane to undulate or even crisply ruffled on the margins. The cells are oblong or rounded in section, each provided with a more or less distinct wall. Although we have only recently become acquainted with it, this seems to be a vernal species. It has been observed in fertile condition in April.

Ulva lobata (Kuetz.) comb. nov.

Phycoseris lobata Kuetzing, Spec. Alg., 1849, p. 477, Tab. Phyc., vol. 6, 1856, p. 10, pl. 27.

Ulva fasciata f. *lobata* Setchell, *in* Collins, Holden and Setchell, Phyc. Bor.-Amer. (Exsicc.), no. 863; Collins, Green Alg. N. A., 1909, p. 216.

Among the *Ulvae* of the Californian coast is one of moderate size (up to 30 cm. or more long, and up to 15 cm. or more broad) which is distinct in general appearance. It is attenuate at the crisped base, broadening above and usually lobed or divided into several broad divisions. The margins are either plane or slightly undulate. Like *U. expansa* it is thicker in the center with palisade-like cells (in section) and thinner on the margins where the cells are nearly square (in section). It bears a striking likeness in every way to Kuetzing's figure (1856, pl. 27) of his *Phycoseris lobata* from Chili. We have, therefore, referred it to his species with some doubt.

Ulva lobata belongs to the same group of species as *U. expansa*, but is generally firmer in substance, slightly thicker, never reaches a great size, and is less deeply or conspicuously ruffled. It is well represented by the specimens distributed in the Phycotheca Boreali-Americana (under no. 863).

The most typical plants are those of the central Californian coast (San Francisco to Monterey). We have referred here, also, one plant from southern California, but with some doubt.

Ulva expansa (Setchell) comb. nov.

Frond ample, pale green, orbicular or broadly elongated, margin deeply ruffled; frond 60–70μ thick in the middle, 38–45μ on the margins; cells, in section, vertically elongated in the middle of the frond (up to 28–30μ long, 10–12μ wide), nearly square in the margins.

Growing on rocks in the lower littoral belt. Puget Sound, Washington, to Mexico (La Paz).

Ulva fasciata f. *expansa* Setchell, *in* Collins, Holden and Setchell, Phyc. Bor.-Amer. (Exsicc.), no. LXXVII; Collins, Green Alg. N. A., 1909, p. 216.

We find along the coast of central California a broad species of *Ulva*, often also long, something like *Ulva latissima* in appearance, yet of a more vivid green color, thicker in the center of the frond and with distinct, broad, ruffled margins. The cells of the thicker center of the frond are distinctly palisade-like in section, while on the thinner

margins they are nearly square. A younger specimen of this plant was distributed by one of us as *Ulva fasciata* f. *expansa* (Phyc. Bor.-Amer., no. LXXVII), but it has seemed, on further study, to belong neither to *Ulva fasciata* Delile nor to the *Ulva fasciata* f. *taeniata* also distributed by one of us (Phyc. Bor.-Amer., no. 809), but described later on in this account as *Ulva taeniata*. We, therefore, describe it as an independent species under the name of *Ulva expansa*.

Ulva expansa, so far as we have observed it, remains attached only for a short time. It soon becomes free and floats or drifts, increasing in size, becoming at times at least 3 M. long and varying in width from 18 cm. to 75 cm. In form and structure it differs from *Ulva latissima* and from all the other species of *Ulva* of our coasts. It comes nearest to *Ulva fenestrata*, as we have described that species, but is little, if at all, perforate. Plants of what appears to be the same species have been found in the Puget Sound region and Howe (1911, p. 490) is inclined to credit here some from La Paz, Mexico.

Ulva dactylifera sp. nov.

Plate 26, figure 1

Thallo sessili aut stipite brevi suffulto; parte basali obovata aut reniformi, crispatissimo, 2–4 cm. alto, e margine superiore 1–6 lobos aut lacinias, simplices aut sparse ramosos et costam definitam ostendentes et marginibus crispatissimis instructos producente, 5–15 cm. high, 0.5–1.5 cm. wide; membrana basali ad marginem 50μ ad medium usque ad 100μ crassa, cellulis e superficie 16–20μ diam. sectione transversali quadratis usque ad 2-plo diam, longioribus; membrana laciniarum marginibus 40–50μ crassa, medio usque ad 190μ crassa, cellulis e superficie 12–16μ diam., sectione transversali quadratis usque ad 5-plo diam. longiores; chromatophoris dimidium externum cellularum implentibus.

Frond sessile or with a very short stipe; basal portion orbicular or reniform, much crisped, 2–4 cm. high, giving rise from the upper margin to 1–6 lanceolate, simple or occasionally branched lobes or laciniae with plane midrib, and much crisped margins, 5–15 cm. high, 0.5–1.5 cm. wide; membrane of basal portion 50μ thick at the margin, up to 100μ thick in the middle, with cells 16–20μ diam. in the surface view, quadrate to 2 times as long as wide in section, membrane of the laciniae 40–50μ thick on margin, up to 190μ thick in the middle, with cells 12–16μ diam. in surface view, quadrate to 5 times as long as wide in section; chromatophore filling the outer half of the cell.

On exposed rocks, uppermost littoral belt. Southern California to Mexico (San Roque?). Type no. 1988, Gardner.

We have along the Californian coast two species related to *Ulva fasciata*, neither of which seems to be exactly like the Mediterranean

species. Both are characterized by long, narrow fronds or laciniae, much thicker along the middle and with thinner, very much crisped margins. One of these, *Ulva dactylifera*, possesses a comparatively broad, though short, undivided basal portion from which arise the several, narrow, elongated, crisped laciniae. Neither the basal portion nor the laciniae show distinctly toothed margins. The other species, *Ulva taeniata*, is either simple, long, slender, plane and dentate below, but with crisped margins above, or divided to the very disk itself into two or three such divisions. The "midrib" portions differ slightly in thickness in the two species and the cells of the "midribs" differ in proportions.

Ulva dactylifera has been distributed under no. 221*b* (sub "*Ulva fasciata*") of the Phycotheca Boreali-Americana. Unfortunately the plants under this number are not uniform. We have examined no. 221*b* in two copies. In one the plant is certainly, although not typically, *U. dactylifera*. In the other it seems rather to be a form of *Ulva Lactuca*.

Ulva dactylifera is nearest to *U. fasciata* f. *costata* Howe (1914, p. 20, pls. 1, 2, figs. 10–23), but differs as to the basal portion, thickness, and possibly also in proportions of cells. It differs from *U. fasciata* Delile, so far as descriptions and figures indicate, in branching, in ruffling, and probably in thickness. It is a very much thinner plant than *U. nematoidea* Bory, judging from the dimensions given by Bornet (1892, p. 36 or 196).

Ulva taeniata (Setchell) comb. nov.

Plate 28

Frond elongated, up to 1 to 2 M. long, simple or split to the very base into long, narrow segments, plane below and coarsely dentate, densely crisped and ruffled on the margins above, with a plane, thicker midrib; membrane up to 140μ thick as to the midrib, and down to 40μ thick on the margins; cells of the midrib vertically elongated, in section, up to two and one-half times as high as broad, but becoming nearly square towards the margins.

On rocks in the lowermost littoral or upper sublittoral belts. Central California (Tomales Bay to Monterey.)

Ulva fasciata f. *taeniata* Setchell, *in* Collins, Holden and Setchell, Phyc. Bor.-Amer. (Exsicc.), no. 862; Collins, Green Alg. N. A., 1909, p. 216.

Ulva taeniata has been found thus far on the coast of central California only, while *U. dactylifera* has been found only on that of southern California. The differences between the two have been enumerated under the latter species. From *U. fasciata* f. *costata* Howe it differs particularly in its basal portion. *Ulva fasciata* Delile seems to be a species nearly if not absolutely plane, while *U. taeniata* is always crisply ruffled. No. 862 of the Phycotheca Boreali-Americana represents this species very well.

Prasiola

There are eight species of *Prasiola* at present accredited to the territory of the Pacific Coast of North America. One of these, *Prasiola crispa* (Lightf.) Menegh., is, we believe, strictly terrestrial, at least so far as our territory is concerned. Another, *P. calophylla* (Carmich.) Menegh., is also terrestrial, but found with us in a marine locality. Three species, *P. borealis* Reed, *P. meridionalis* sp. nov., and *P. delicata* sp. nov., are strictly marine. One species, *P. Gardneri* Collins, has been removed to the genus *Merismopedia* (*M. Gardneri* Setchell), while three species, *P. fluviatilis* (Sommerf.) Aresch., *P. mexicana* J. Ag., and *P. nevadensis* sp. nov., are inhabitants of cold fresh-water streams.

Prasiola mexicana J. Ag. (1847, p. 6) is based upon specimens collected in Mexico by Professor Liebmann of Copenhagen. The type locality is Santa Maria Alpatlachna in Mexico. The habitat is turbulent mountain streams. The habit is that of a broad plant, umbilicate at the base and laciniate and irregularly crispate. Agardh simply adds that the areolae are regularly quaternate. No mention is made of the presence of intercellular lines, "*viae interstitiales*," in this first description. Jessen (1848, pp. 19, 20, pl. 1, figs. 17–20) gave a more ample description and illustrations from materials and information provided by Liebmann. Lagerstedt (1869, p. 26) redescribed the species, but drew his information largely, if not entirely, from Bolivian specimens. J. G. Agardh (1882, p. 84) added nothing in his final review of the genus *Prasiola*.

Thus far the specimens from our mountain streams have all been referred to *Prasiola mexicana* J. Ag. (1847, p. 6), a species with broad fronds, umbilicate or nearly so at the base, and arising from a disk, possibly later developing secondary rhizoidal outgrowths of attachment on the decumbent base. The color is dark green and the laciniae

have crisped or ruffled edges. This description is taken largely from Jessen (1848, p. 19, pl. 1, figs. 17–20), who, as noted above, received his materials from the type collection directly from Liebmann, the original collector. Unfortunately we have not been able to examine any of the type material and, consequently, must judge our plants entirely from the point of view of the descriptions and figures. From this point of view it seems safe to refer most of the various specimens accessible to us to *P. mexicana*.

Under *Prasiola mexicana* have thus been referred specimens from Montana (Tilden, Amer. Alg., no. 129), Wyoming (Tilden, *loc. cit.*, no. 555*a*) and Oregon (Tilden, *loc. cit.*, no. 555*b*, and Collins, Holden and Setchell, Phyc. Bor.-Amer., no. 1186). The species is represented in the Herbarium of the University of California by specimens from Washington (no. 132922, collected by Professor T. C. Frye in the Ehoha River in the Olympic Mountains), from Oregon (no. 98182, from McCleary Canyon near Portland, collected by A. S. Foster; nos. 98181 and 98183, collected near Eugene and near Forest Grove respectively by Professor A. R. Sweetser), while in California it has been collected in Crane Creek above El Portal at an altitude of 4000-4500 feet (Gardner, no. 4466). It is reported by Wolle (1887, p. 107, pl. 91, fig. 24) from Colorado, where it was collected by T. S. Brandegee. It has also been collected in the Diamond range of mountains in eastern Nevada, where it was found by Sereno Watson and described by Horatio C. Wood (1871, p. 415, 1873, p. 182) under the name of *Ulva merismopedioides*. A portion of the type (or cotype) has been examined and there seems little question as to the identity of Wood's species and those we are assigning to *Prasiola mexicana* J. Ag. The fragment of the type examined and from which our figures (cf. pl. 21, figs. 8–10) are drawn for comparison was communicated to us by Frank S. Collins, having been received by him from the United States National Herbarium. Collins (1903, p. 17) placed the *Ulva merismopedioides* Wood under *Monostroma quaternarium*, but later, as he writes us, made a second examination of the material and found something seemingly different from what he had examined previously and upon which he had based his opinion. The fragment examined by us is clearly *Prasiola mexicana* as we understand that species. The cross-section of Wood's plant, however, differs from the description of Wood in that the cells (cf. Wood, 1873, p. 182) are not in a single layer, but in two to several, as a glance at our illustrations (cf. pl. 21, figs. 9, 10) will show.

In connection with cross-sections of *Prasiola mexicana,* it may be said that the various specimens agree very well as to the number and arrangement of cells but differ somewhat in width of section. In width the sections vary from 24μ to 52μ, but the increase in thickness is more or less associated with the development of the so-called aplanospores. We find these arising in greater numbers from a single cell than any description thus far indicates for any species of *Prasiola.* Lagerheim has described and figured them for *Prasiola mexicana* var. *quitensis* Lagerheim (1892, pp. 370–372, pl. 20, figs. 15–22). He found either a single layer of tetrads (*loc. cit.,* fig. 18) or two layers of tetrads (*loc. cit.,* fig. 20) in the membranes of his variety. In our specimens we find the double row of tetrads (cf. pl. 21, figs. 3–7), and also double rows of tetrads intermingled with groups where the horizontal divisions have proceeded farther, as they do in antheridial formation in certain species of *Porphyra.* The majority of sections show the two kinds (or stages in development) of these bodies intermingled. We feel it necessary to consider these bodies as aplanospores until further investigation can shed more light as to their fate, but the resemblance between them and the species of *Porphyra,* as well as the resemblances in cell structure, particularly as regards the shape and position of the chromatophore, suggests strongly the possibility of a nearer relation to the Bangiales than to the Ulvales and a remote (?) possibility that we may be dealing here with antheridia and a very simple type of cystocarp.

Comparing our specimens with the descriptions and figures of Agardh and Jessen, we believe them to be true *Prasiola mexicana,* and comparing them with Lagerheim's descriptions and figures we are inclined to agree with him that the Equador plant is different, possibly even specifically.

One of us (Setchell) has found a *Prasiola* in Crane Creek (Mariposa County, California), between Big Meadow and McCauley's, which differs so much from *P. mexicana* that it seems desirable to describe it as new. It differs from *P. mexicana* in habit, color, and structure. It is always elongated (cf. pl. 21, figs. 11–13), while *P. mexicana* is broad and umbilicate. In color it is light, almost yellow-green, instead of the darker green characteristic of *P. mexicana.* In surface view (cf. pl. 21, figs. 14–16) the smaller groups of cells are more distinctly placed and are further marked off into areas by delicate lines (or borders) in the enclosing jelly. The sections (cf. pl. 21, figs. 17, 18) are as broad as the narrower sections of *P. mexicana,* being 17μ to 25μ

or 26μ wide. The aplanospores form a simple series of tetrads only and show no disposition to proceed further. On account of these differences it seems best to describe these plants as belonging to a new species, *Prasiola nevadensis*. It is to be recorded and is of decided significance in this connection that the other one of us (Gardner) has collected characteristic *Prasiola mexicana* in the same stretch of the same stream, at the same season but in a different year. It may be, therefore, that our new species may be found to be included among the stages in the development of, or states of, *P. mexicana*. It seems so distinct, however, that we venture to describe it as new and specimens will be distributed in a fascicle of the Phycotheca Boreali-Americana soon to be issued.

Prasiola nevadensis comes much nearer to *P. fluviatilis* (Sommerf.) Aresch. than to *P. mexicana*. It differs from *P. fluviatilis* so far as we may determine from descriptions, figures and scanty specimens available to us, in being broader and not tapering regularly from above toward the base. We do not know much about the structure of *P. fluviatilis*, but suspect that the general character and arrangement of cells may closely resemble those of our *P. nevadensis*. Our plant may be closer to *P. fluviatilis* var. *Hausmanni* Grun., in that it is a broader species than typical *P. fluviatilis*, but further comparison is impossible. We append the following diagnosis:

Prasiola nevadensis sp. nov.

Plate 21, figures 11–18

Thallis gregariis, angustis, 2–3 cm. longis, 0.5–1 cm. latis, oblongis usque ad oblanceolatis, e basibus latis oriundis, primo disco minuto, aetate provecta, rhizoidibus e basi decumbente emissis affixis, dilute viridibus, marginibus undulatis et crispatissimis; membrana 14–25μ crassa; cellulis in gregibus parvis e superficie visis quaternis, rotundis aut augulatis, laxe positis et in areolas indistinctas segregatis, in sectione transversali rotundis usque ad valliformibus; viis interstitialibus distinctis nullis; aplanosporis in serie singula, quaternis.

Thalli gregarious, narrow, 2–3 cm. long, 0.5–1 cm. wide, oblong to oblanceolate, from a broad base, attached at first by a small disk, later by rhizoids from the basal portion, pale green, with margins undulate and very much crisped; membrane 14–25μ thick; cells in small groups of tetrads as seen from the surface, rounded or angular, loosely placed, forming indistinct areoles, but without interstitial lines, cells in transverse section rounded to elongated vertically; aplanospores (?) in a single layer of tetrads.

In rapid waters of Crane Creek, Foresta townsite, Mariposa County, California, at 3500–4000 feet altitude. Type no. 6507, Setchell.

Prasiola meridionalis sp. nov.

Plate 25, figure 2

Thallo usque ad 7 mm. alto, stipiti brevi latoque in laminam latam, cordatam et rosulatam aut cucullatam abeunte, sordide viridi; cellulis neque in areolis distinctis ordinatis neque per vias interstitiales separatis; membrana 40–45μ crassa, in sectione transversali cellulas 14–18μ altas et 7–8μ latas marginibus latis hyalinisque (usque ad 13μ crassis) ostendente; akinetis dispersis, magnis, parietibus crassis; aplanosporis probabiliter 128–512 ($4 \times 4 \times 8$ aut $8 \times 8 \times 8$) in aplanosporangio singulo.

Frond up to 7 mm. high, with short and broad stipe, soon expanded into a broad, cordate, rosulate or cucullate blade, dirty green; cells neither arranged in distinct areolae nor separated by interstitial lines; membrane 40–45μ thick, section showing cells 14–18μ high and 7–8μ wide with broad hyaline margins (up to 13μ thick); akinetes scattered, large, thick walled; aplanospores probably 128–512 ($4 \times 4 \times 8$ or $8 \times 8 \times 8$) from a single aplanosporangium.

On exposed rocks or rocky islets above the high-water mark but exposed to the force of the waves. Washington (Friday Harbor and Neah Bay) to central California (entrance to Tomales Bay). Type no. 3824, Gardner.

The specimens taken as the type of this species were collected by one of us (Gardner) at Neah Bay, Washington. We are also inclined to refer here specimens collected at "Minnesota Reef" at Friday Harbor, Washington, and at the entrance to Tomales Bay, California. In the last two localities the species is associated with *Gayella constricta*. Cultures, however, strongly indicate the independence of the two plants from one another.

Prasiola meridionalis comes near to *P. borealis* Reed, but the frond of the latter is areolate and with more or less distinct intercellular lines. *P. borealis* is, so far as found, infested with a fungus (*Guignardia alaskana* Reed), while none of the three collections of *P. meridionalis* shows any trace of such a parasite.

Prasiola delicata sp. nov.

Plate 22, figure 3*a-f*, and plate 25, figure 1, and plate 24, figure 8

Thallo 1–1.5 mm. alto, lato et breviter stipitato, in laminam late oblongam aut cordatam expanso, marginibus crispatis et involutis, atro-cyaneoviridi; membrana 17–20μ crassa, cellulis neque in areolas distinctas ordinatis neque per vias interstitiales separatis; akinetis non visis; aplanosporis usque ad 512 e cellula singula ($8 \times 8 \times 8$) sed frequenter tantum 128; cellulis valliformibus, in sectione transversali verticaliter 10–12μ, 2-plo aut ultra diam. longioribus.

Frond 1–1.5 mm. high, broad and shortly stipitate, expanding directly and abruptly to broadly oblong or cordate, margins crisped and inrolled, dark bluish green; membrane 17–20μ thick, cells not grouped into distinct areolae and not separated by interstitial lines; akinetes not seen; aplanospores up to 512 from a single cell ($8 \times 8 \times 8$), but often only 128; cells palisade-like and 10–12μ in vertical diameter, in section twice or more times as high as broad.

Growing at or near the upper tide mark on rocky islets. Sitka, Alaska. Type no. 3981, Gardner.

Prasiola delicata has a decidedly thinner membrane than any other of our marine species, shows little areolation, and has a larger number of aplanospores formed within a single aplanosporangium. These characters seem to indicate its just claim to be considered a distinct species.

Entocladia cingens sp. nov.

Plate 23, figure 7

Thallo textum pseudoparenchymaticum filamenta hospitis cingens et intus membranam, sed filamenta marginalia ad longitudinem hospitis parallela ostendens mox formante; cellulis centralibus fere isodiametricis, 5–8μ diam., tardiore augescentibus et in sporangia transformatis; cellulis filamentorum liberorum marginalium 3–4μ diam., 2–3-plo diam. longioribus, terminalibus longis, conicis.

Thallus early forming a pseudoparenchymatous tissue surrounding the filaments of the host within the membrane, having a few marginal filaments extending parallel with the long diameter of the host; cells in the center of the thallus nearly isodiametric, 5–8μ diam., enlarging later to form sporangia; cells of the free marginal filaments 3–4μ diam., 2–3 times as long as the diameter, terminal cells long, conical.

Growing within the membrane of *Chaetomorpha californica* Wille. Southern California (Ocean Beach, near San Diego), December. Type no. 3528*a*, Gardner.

The plants of this species seem to be nearing maturity in December, since a few empty cells in the center of the thallus were found from which reproductive bodies probably had escaped. Aside from this condition, nothing further is known of its method of reproduction.

Entocladia cingens is placed in this genus on account of the resemblance of the vegetative development to that of the type species, *E. viridis* Reinke, and because it has the same endophptic habit as has that species. It differs from *E. viridis* in having the branching filaments more closely coalescent, the enlarging cells in the main part of the thallus soon forming a pseudoparenchymatous tissue, leaving only a few free marginal filaments.

E. viridis, E. codicola, and *E. cingens* form a well connected series, using the vegetative characters as a basis. The first named species has a rather wide spreading thallus, composed of relatively sparsely branching filaments, scarcely, if at all, coalescing in the center. In the second the filaments coalesce freely in the center so that at least half of the thallus is formed into a pseudoparenchymatous tissue at the time of reproduction, but leaving an abundance of free branching marginal filaments. The thallus of the third is almost wholly transformed into a pseudoparenchymatous tissue at maturity leaving only a few free marginal filaments.

Entocladia codicola sp. nov.

Plate 24, figures 7*a*, 7*b*

Filamentis laete viridibus, profuse ramosis, maturitate stratum continuum centrale ad peripheriam terminos liberos et attenuatos exhibens formantibus; cellulis juvenis 3–4μ diam., 1–2.5-plo diam. longioribus, terminantibus gracilibus et conicis; cellulis thalli centralibus 5–8μ diam.; pyrenoidibus singulis; generatione ignota.

Filaments light green, branching profusely, at maturity forming a continuous layer in the center of the mass with many tapering free ends around the margin; young cells 3–4μ diam., 1–2.5 times as long, terminal cells slender and conical; cells in the center of the thallus 5–8μ diam.; pyrenoid single; reproduction unknown.

Growing in the membrane, at the tips of the utricles of *Codium fragile.* Central and southern California. Type no. 4121, Gardner.

Entocladia codicola seems closely related to *Entocladia viridis* Reinke (1879, p. 476, pl. VI, figs. 6–9), found growing in the membrane of *Derbesia;* but it is a larger plant with the filaments much more compact in the center, forming in fact a pseudoparenchymatous disk with free filaments around the margin. The cells are shorter than those of *E. viridis,* some being even shorter than the diameter. In the pseudoparenchymatous character of the center of the disk-like frond it resembles *Entocladia Flustrae* Reinke (1888, p. 241, nomen nudum, 1889, p. 31, pl. XXIV, 1889*a,* p. 86), but the dimensions given for that species are in general greater than those in ours. Reproductive bodies have been observed in the cells of the central portion of the disk in *E. codicola,* but the nature of these, their method of escape, and their subsequent behavior have not been determined. Until more is known concerning these later phases of the plant, its proper placing must remain somewhat in doubt. It is here provisionally placed with *Entocladia* on account of its endophytic habit of growth,

rather than with *Epicladia*, which has the habit of growing on the outside of the host. This habit of growth seems to be the only one by which the two genera are distinguished as far as the diagnoses reveal. Little, however, is known concerning the reproduction in *Epicladia*, and until the matter can be cleared up it can have but little claim to generic distinction. Reinke expressed doubt as to the validity of the genus when he diagnosed it (1889). Collins (1909) has retained both genera, and under *Endoderma* (*Entocladia*) has included two species, viz., *E. pithophorae* West and *E. polymorphum* West, which are epiphytic, and thus, as he remarks (*loc. cit.*, p. 280), "connects *Endoderma* with *Epicladia*, but the filaments do not unite to form a definite disk."

Entocladia codicola seems to be confined to the coast of California and to the above mentioned host plant, at least, examination of considerable material of different species of *Codium* in different localities ranging from Sitka, Alaska, to southern California has not revealed its presence elsewhere.

Internoretia gen. nov.

Thallus endophyticus, e filamentis profuse ramosis, primo cellulis in serie simplici per divisiones apicales verticaliter ad longitudinem positas augescentibus, tardiore per divisiones obliquas et longitudinales, filamenta cylindrica cellulis numerosis composita formantibus; filamenta ramos ad angulos rectos emittentia, ramis anastomosantibus; chromatophora parietalis, pyrenoidibus singulis; generatio ignota.

Thallus endophytic, consisting of profusely branched filaments, at first of a single series of cells increasing by apical divisions perpendicular to the long diameter, but later by oblique and longitudinal divisions, building up cylindrical threads composed of numerous cells in cross diameter; branching at right angles, anastomosing, forming a network; chromatophore parietal, with one pyrenoid; reproduction unknown.

The genus *Internoretia* is proposed for a peculiar endophyte found by Professor T. C. Frye, growing within the membranes of *Porphyra Naiadum*. Its reproduction not having been determined, it is among the numerous form-genera of uncertain position and placed provisionally among the Chaetophoraceae. It resembles *Pseudodictyon* Gardner and *Zygomitus* B. and F. From the former it differs in forming solid filaments several cells in thickness. From *Zygomitus*, *Internoretia* differs in the greater regularity of its solid portions and in the more uniform network brought about by the regular giving off of branches at right angles.

Internoretia Fryeana sp. nov.

Plate 23, figures 3–6

Cellulis filamentorum terminalium 3.5–5μ diam., 3–5-plo diam. longioribus, apicalibus conicis; cellulis partium thallorum vetustiorum isodiametricis, angularibus; aliter ut in generi.

Cells of the terminal filaments 3.5–5μ diam., 3–5 times as long, apical cell conical; cells of the older part of the thallus isodiametric, angular; otherwise as the genus.

Growing within the membrane of *Porphyra Naiadum*. Friday Harbor, Washington, July. Type no. 4260, Gardner.

This most interesting little plant is as yet known only from the collections and observations of Professor T. C. Frye. It generally occurs in such abundance as to discolor the host plant. In some years it is very common, discoloring most of the plants of *Porphyra* in the neighborhood of the Puget Sound Marine Station, while in other years it is difficult to find any plants at all.

Pseudulvella prostrata (Gardner) comb. nov.

Growing on the basal portion of *Iridaea laminarioides*. Central California (Lands End, San Francisco).

Ulvella prostrata Gardner, New Chlorophyceae, 1909, p. 373, pl. 14, figs. 1, 2; Collins, Green Alg. N. A., 1909, p. 287; Collins, Holden and Setchell, Phyc. Bor.-Amer. (Exsicc.), no. 1629.

Recent observation has revealed the presence of a pyrenoid in each cell of the plant under consideration, a character not belonging to the genus *Ulvella*. This character militates against placing it in that genus. As found growing on *Iridaea*, it has no penetrating rhizoids, thus differing in this respect from the genus *Pseudopringsheimia*, to which it seems closely related. Nothing has yet been learned regarding reproduction. Considered in the light of our present knowledge, *Pseudulvella* seems to be the genus most appropriate for its reception.

Pseudulvella applanata sp. nov.

Thallo tenui parenchymatico, per incrementum marginale ad mm. plura augescente, laevi et nitido, 45–55μ crasso, laete viridi; cellulis in series verticales, proxime regulares positis, proxime isodiameitricis, acute angulatis, 6–7.5μ diam.; chromatophoris parietem cellularum tegentibus, pyrenoidibus singulis; zoosporangiis (?) e cellulis superficialibus leviter transformatis oriundis; generatione ignota.

Thallus thin, parenchymatous, spreading by marginal growth, expanded to several mm. in diam., smooth and glossy, 45–55μ thick; color grass green; cells in fairly regular vertical rows nearly isodia-

metric, sharply angled, 6–7.5μ diam.; chromatophore covering the cell wall provided with one pyrenoid; zoosporangia (?) slightly modified surface cells; reproduction unknown.

Growing on the shells of *Littorina planaxis* Nutt. Central California. Type no. 3597, Gardner.

Littorina planaxis Nutt. is very abundant in small tide pools and in moist places along high-tide level from Sitka to San Diego. *Pseudulvella applanata* has been studied only on material found along the coast of central California, but it is presumed to have a much wider distribution.

Its presence on the host is readily recognizable by the expanded, grass green, glossy appearance of the surface of the shell. Microscopically it may readily be distinguished from all other described species of the genus by its very small, closely compact, parenchymatous cells, and the seeming absence of radiating filaments composing the basal layer. It spreads over the host by tangential and by radial divisions of the peripheral cells, at least the process can thus be described when the plant is of considerable size. It probably starts on the very young host, and doubtless many plants early coalesce to form a confluent thallus. We have not been able to ascertain the nature of the early developmental stages, although very small shells have been examined.

Reproductive bodies have been seen to escape from the surface cells. Whether these are zoospores or gametes, the number of cilia they possess and their behavior after escaping are subjects for further investigation.

The three species of Pseudulvella known from the western coast of North America may be arranged, so far as the basal layer is concerned, in the following sequence: *P. prostrata*, with distinctly radiating basal filaments which branch rather frequently and which are comparatively loosely coalescent; *P. consociata*, with indistinctly radiating basal filaments closely coalescent; and *P. applanata* with a parenchymatous basal layer.

Pseudulvella consociata sp. nov.

Plate 24, figures 4–6

Thallo magnitudine et peripheria irregulari, 100–140μ crasso, per filamenta irregularia et radiantia augescente; filamentis mox coalescentibus et parenchymaticis, atroviridi; filamentis erectis dense adhaerentibus, 7–10μ diam., cellulis prope cylindricis, forma leviter irregularibus, 1–2-plo diam. longioribus; zoosporangiis (?) terminalibus, pyriformibus usque ad sphaericis, 8 zoosporas emittentibus.

Thallus irregular in size and in outline, 100–140μ thick, increasing by irregular and obscurely radiating filaments early coalescing and becoming parenchymatous; color dark green; erect filaments firmly coalescent, 7–10μ diam., cells nearly cylindrical, slightly irregular in form, 1–2 times as long as the diameter; zoosporangia (?) terminal, pyriform to spherical, producing 8 zoospores.

Growing on the shells of *Ilyanassa obsoleta* Say. Central California (Bay Farm Island, Alameda). Type no. 4268, Gardner.

The shells of *Ilyanassa obsoleta* Say. were introduced some years ago along with oysters from the Atlantic coast of North America, and possibly the plant here described was introduced with the host.

A comparison of this species with others will be found included in the discussion under *P. applanata.*

Pseudopringsheimia apiculata sp. nov.

Plate 22, figures 1, 2

Thallis minutis, 145–160μ crassis, dum solitariis hemisphaericis, sed frequenter dense gregariis et stratum continuum 2–3 mm. diam. formantibus, laete viridibus; filamentis erectis 8–12μ diam., 9–12 cellulis cylindricis aut leviter tumidis compositis; zoosporangiis (?) 8 zoosporas emittentibus, terminalibus, leviter tumidis, convexis usque ad conspicue apiculatis; zoosporis (?) 4-ciliatis.

Thallus minute, 145–160μ thick, hemispherical when alone, but often with many crowded closely together forming a continuous stratum 2–3 mm. diam.; color bright green; erect filaments 8–12μ diam., composed of 9–12 cylindrical or slightly swollen cells; zoosporangia (?) producing 8 zoospores, terminal, slightly swollen, varying from convex to decidedly apiculate; zoospores (?) 4-ciliated.

Growing on the rhachis and the cysts of *Egregia Menziesii.* Central California. Type no. 4361, Gardner.

Pseudopringsheimia apiculata is closely related to *P. confluens* (Rosenv.) Wille. The most conspicuous difference is to be found in the shape and size of the zoosporangia, if the terminal reproductive cells are to be designated as such. Those of *P. confluens* are long and comparatively narrow, and produce 30 to 40 zoospores, while in *P. apiculata* they are shorter, somewhat swollen, mostly with a pronounced terminal projection, and produce about 8 zoospores. These reproductive bodies are very small and it is exceedingly difficult to determine their number of cilia. On one occasion four cilia were observed, but the reproductive bodies seemed a little larger and somewhat more irregular in form than the average. These may have been the zygotes which had been formed by the fusion of 2-ciliated gametes and which had not yet come to rest.

Gomontia polyrhiza (Lagerh.) B. and F.

Plate 24, figure 1

"Sporangia" irregularly and broadly clavate to nearly cylindrical, up to 150μ diam., and 240μ long, producing usually several blunt, at times slightly branched, rhizoids at the smaller end.

Growing in clam shells. Neah Bay, Washington.

Bornet and Flahault, Note sur deux nouveaux genres d'algues perforantes, 1888, pp. 161–163 (as to combination only). *Codiolum polyrhizum* n. sp. Lagerheim (at least in greater part).

The above description is taken in part from the original of Lagerheim and in part from the material collected at Neah Bay. The material from which Lagerheim drew his description was apparently in the sporangial stage exclusively, at least he did not recognize a sterile or vegetative stage. The Neah Bay material, collected in May, is likewise in a reproductive stage, or if the vegetative stage is present it and the sporangial stage could not be identified as belonging to the same species, hence the incompleteness of the description.

The sporangia approximate so closely to the figures (especially figs. 10, 11) and the description of Lagerheim as to make it sufficiently safe to ally our plant with his and to keep it distinct from the *G. polyrhiza* of Bornet and Flahault (*G. Bornetii* S. and G.).

The filaments of this species have been examined by us in a specimen distributed by Reinbold from Kiel. Reinbold's specimens have "sporangia" largely of the *Codiolum*-type, both old and young, but is also has an occasional "sporangium" of the Acarid-type (apparently good *G. Bornetii*). Since Reinbold's locality is not far distant from Lagerheim's type locality, it seems extremely probable that his plant is true *G. polyrhiza*. The filaments in Reinbold's specimens are so close to those of *G. Bornetii* as figured by Bornet and Flahault (*loc. cit.*) as to be indistinguishable.

Gomontia Bornetii nom. nov.

Horizontal filaments irregular, much branched, erect filaments with clavate ends, less branched; cells 4–12μ, most frequently 6μ diam., 15–55μ long, cylindrical to more or less swollen and crooked; "sporangia" variable and irregular in form, 8–125μ wide, 150–200μ long, having numerous, mostly simple rhizoids arising principally on one side but occasionally promiscuously scattered all over the sporangia; zoospores of two sorts, one 3.5μ wide and 5μ long, the other 5–6μ wide and 10–12μ long, development unknown; aplanospores 4μ diam.

Growing in clam shells. Neah Bay, Washington.

Gomontia polyrhiza Bornet and Flahault, Notes sur deux nouveaux genres d'algues perforantes, 1888, pp. 161–163 (not *Codiolum polyrhiza* Lagerheim).

Bornet and Flahault (1889, p. 9) distinctly state that the greatest dimensions of the "sporangia" in their specimens are 120μ for height and 75μ for width, and mention that Lagerheim found "sporangia" in the specimens up to 240μ in height and 60μ in breadth. We judge, therefore, that the *Codiolum*-type of "sporangium" which Lagerheim figures (1885, pl. 28, figs. 10, 11 in particular) and describes (*"plerumque plus minus elongatis," loc. cit.,* p. 22) was not to be found in the French material and certainly is not illustrated by Bornet and Flahault, unless figure 9 on plate 7 may represent it. The type of "sporangium" illustrated by Bornet and Flahault (1889, pls. 7, 8) belongs to the shorter and broader type, the Acarid-type as it may be called, and has blunt, simple or slightly branched rhizoids. Lagerheim (*loc. cit.,* pl. 28, figs. 7, 8, 12, 13) has also figured "sporangia" of the Acarid-type and probably found a mixture of species in the shells he examined. Since, however, he emphasizes the elongated, or *Codiolum,* type of sporangia, it seems best to reserve his specific name for the species with the *Codiolum*-type of "sporangium" and assign the new specific name (*Bornetii*) to the species having the Acarid-type of "sporangium" and with blunt, rather stout, simple or, at most, slightly branched rhizoids.

The filaments of *G. Bornetii* are well represented by Bornet and Flahault (1889, pl. 6, figs. 1–8) and by their usually large number of short, blunt or almost bulbously enlarged branchlets and their compact massing make a characteristic appearance after decalcification. They are very similar to those of *G. polyrhiza,* as far as we can determine, but somewhat different from those of *G. habrorhiza,* although this difference is not readily described.

While we find what seems referable to *G. Bornetii* in the Puget Sound region and that of central California, we desire more abundant and more decisive material before we can determine this.

Gomontia habrorhiza sp. nov.

Plate 24, figures 2, 3*a*, 3*b*, 3*c*

Filamentis repetite et irregulariter ramosis; cellulis forma magnitudineque maxime variabilibus, typice cylindricis, 4–7μ diam., 2–8-plo diam. longioribus, chromatophoris pyrenoidibus destitutis, cellulam totam implentibus; "sproangiis" (gametangiis ? aut aplanosporangiis ?) angustis aut latis, obtuse conicis, 50–70μ altis, 25–60μ latis, in

latere inferno rhizoidibus multis gracillimis, attenuatis et dendritice ramosis indutis; generatione ignota.

Filaments repeatedly and irregularly branched; cells very variable in form and size, typically cylindrical, 4–7μ diam., 2–8 times as long; chromatophore without pyrenoids, filling the cell; "sporangia" narrow to wide, bluntly conical, 50–70μ high, 25–60μ wide, developing many very slender, attenuate, dendritically branched rhizoids from the lower side; reproduction unknown.

Growing on dead clam shells. Neah Bay, Washington. Type no. 3825, Gardner.

In a *Gomontia* inhabiting certain shells from Neah Bay we have found all the "sporangia" of the Acarid-type and with the processes or rhizoids slender, branched, and attenuated to a point. The "sporangia" seem so distinct from those of *G. Bornetii* that we describe the plant possessing them as new. In some shells we have found the "sporangia" of this species intermingled with others. The vegetative filaments of *G. habrorhiza* seem less entangled and slightly larger than those of either *G. polyrhiza* or *G. Bornetii*.

Gomontia caudata sp. nov.

Plate 23, figures 1, 2

Filamentis brevibus, parce ramosis; cellulis 5.5–6.5μ diam., 2–12-plo diam. longioribus; chromatophoris cellulas terminales et "sporangia" juvena implentibus, in cellulis vetustioribus interruptis; pyrenoidibus inconspicuis; "sporangiis" (gametangiis ? aut aplanosporangiis ?) clavatis, 50–70μ latis, 160–200μ longis, inferne ad rhizoide singula attenuatis, parietibus maturitate crassis, hyalinis, homogeneis; rhizoidibus saepe maxime incrassatis striatisque.

Filaments short, sparsely branched; cells 5.5–6.5μ diam., 2–12 times as long; chromatophore covering the terminal cells and young "sporangia," broken in the older cells; pyrenoids inconspicuous; "sporangia" clavate, 50–70μ diam., 160–200μ long, tapering to a single rhizoid below with thick, hyaline, homogeneous wall at maturity; rhizoid often becoming much thickened and striated.

Growing in shells of *Mytilus californicus* Conr. Neah Bay, Washington. Type no. 3825, Gardner.

We have found in shells of the larger edible mussel of our coast a *Gomontia* with filaments seemingly less abundantly branched and "sporangia" (aplanosporangia ?) with very thick walls and a single long rhizoid (cf. pl. 23, figs. 1, 2). These "sporangia" bear a certain resemblance to the "cells" figured by Lagerheim (1885, pl. 28, figs. 4, 6), but are, at least, thicker walled. The fact which seemed to indicate distinctness was that only this type of "sporangium" was found in the shells examined.

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PLATE 21

Prasiola mexicana J. Ag.

Herb. Univ. Calif., no. 91181, collected near Eugene, Oregon, by Professor A. R. Sweetser, May, 1903.

Fig. 1. Habit of typical plant. × 0.5.

Fig. 2. Surface view of thallus lobe. × 375.

Fig. 3. Transverse section showing double layer of tetrad-type of aplanospore (?) formation. × 375.

Fig. 4. Similar section showing both tetrad and "antheridial" type of aplanospore (?) formation. × 375.

Fig. 5. Similar section to that of figure 3, but less regular. × 375.

Herb. Univ. Calif., no. 91182, collected near Portland, Oregon, by H. A. Foster.

Fig. 6. Transverse section showing single layer of tetrad-type of aplanospore (?) formation. × 375.

Fig. 7. Transverse section showing "antheridial" type of aplanospore (?) formation. × 375.

No. 1545, U. S. Geol. Surv., collected in the Diamond Range, Nevada, by Sereno Watson and type collection of *Ulva merismopedioides* Wood.

Fig. 8. Surface view of lobe of thallus. × 375.

Fig. 9. Transerve section showing double layer of tetrad-type of aplanospore (?) formation. × 375.

Fig. 10. Similar section showing "antheridial" type of aplanospore (?) formation. × 375.

Prasiola nevadensis S. and G.

No. 6507, collected in Crane Creek, Foresta townsite, Mariposa County, California, by W. A. Setchell, June, 1914.

Fig. 11. Habit of young plant. × 0.5.

Fig. 12. Habit of young plant. × 0.5.

Fig. 13. Habit of older plant. × 1.

Fig. 14. Surface view of lobe of thallus. × 375.

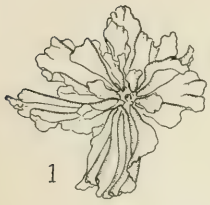
Fig. 15. Surface view of lobe of thallus. × 375.

Fig. 16. Surface view of portion of thallus. × 375.

Fig. 17. Transverse section showing cells probably on the way to aplanospore (?) formation. × 375.

Fig. 18. Similar section showing tetrad-type of aplanospore(?) formation. × 375.

All the figures of this plate were drawn by Dr. Helen M. Gilkey under the direction of W. A. Setchell.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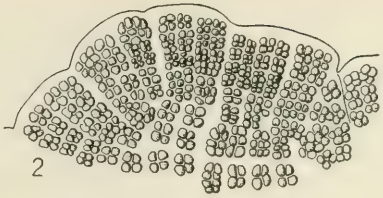
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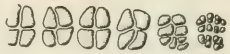
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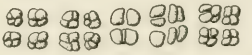
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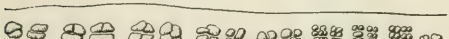
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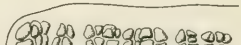
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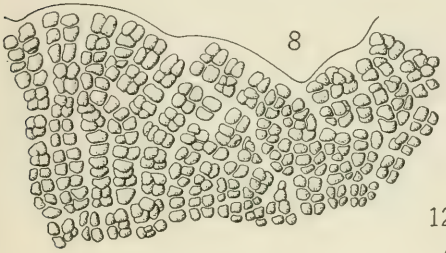
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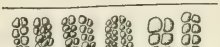
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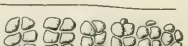
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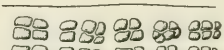
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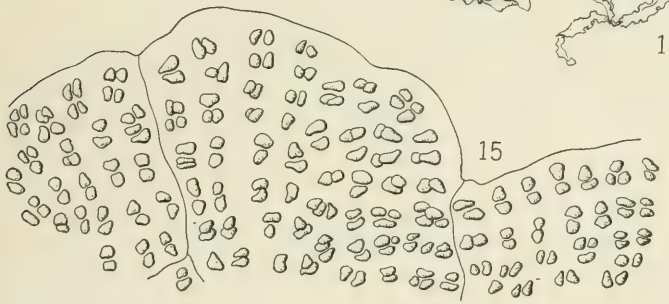
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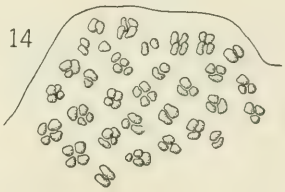
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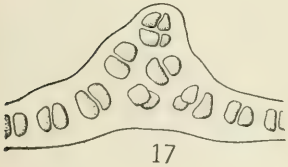
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PLATE 22

Pseudopringsheimia apiculata S. and G.

Fig. 1. A section through the thallus of a mature plant perpendicular to the host. × 250.

Fig. 2. A section through the thallus of a young plant. × 250.

Prasiola delicata S. and G.

Fig. 3. *a-f*, series of different forms of plants. × 10.

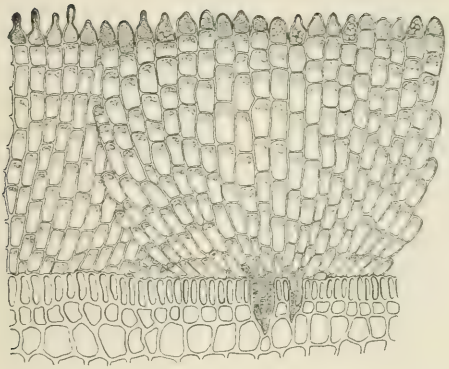
Ulva rexata S. and G.

Fig. 4. A group of plants showing different shapes and sizes. × 1.

Fig. 5. A group of mature plants showing the presence of the parasitic fungus *Guignardia Ulvae* Reed. × 3. Taken from Reed, 1902, pl. 15, fig. 1.

Fig. 6. A cross-section showing the presence of fungal hyphae in the medulla. × 250.

Fig. 7. A surface view. × 250.



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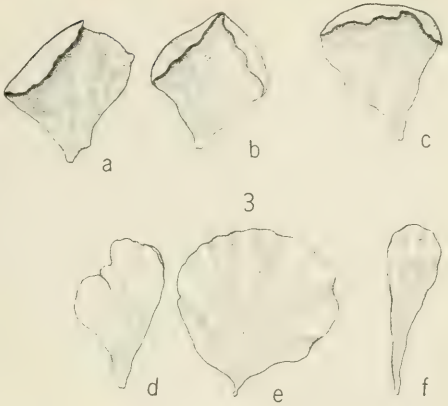

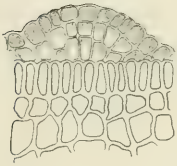

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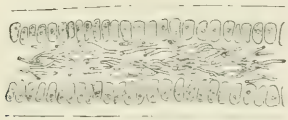

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PLATE 23

Gomontia caudata S. and G.

Fig. 1. Two pieces of filaments. × 400.

Fig. 2. *a-d,* different stages and forms of "sporangia." × 400.

Internoretia Fryeana S. and G.

Fig. 3. A surface view of the host plant showing the method of permeation and branching of a few terminal filaments. × 375.

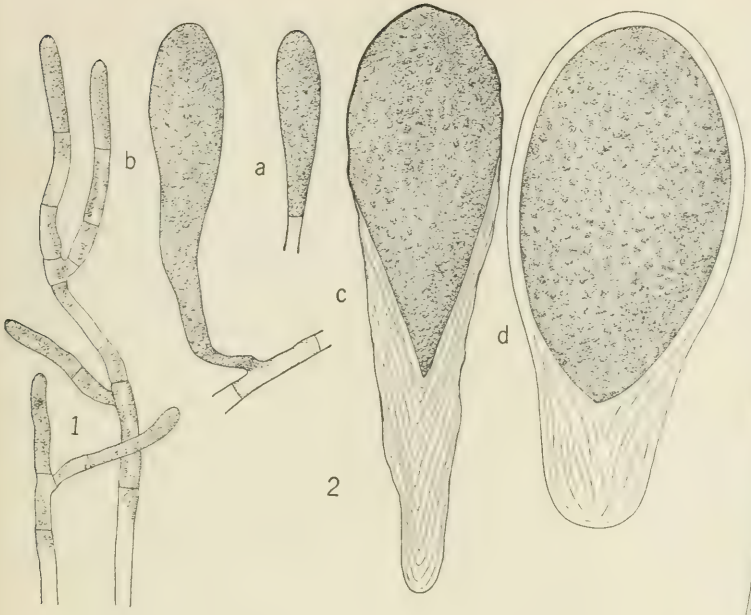
Fig. 4. A stage slightly in advance of figure 3 showing cell divisions in planes parallel to the long diameter of the cells. × 375.

Fig. 5. A stage in development nearing maturity. × 375.

Fig. 6. A cross-section of the host cutting the filaments of *Internoretia* at right angles to their long diameter. × 375.

Entocladia cingens S. and G.

Fig. 7. A plant growing in the membrane of *Chaetomorpha californica* and nearing maturity. × 250.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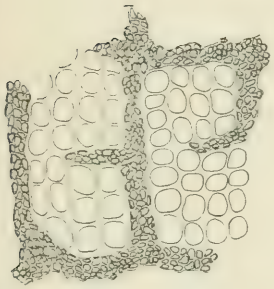
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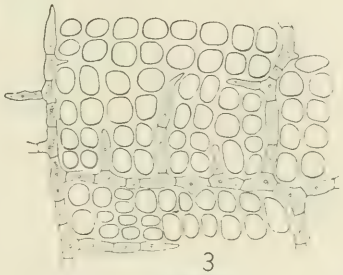
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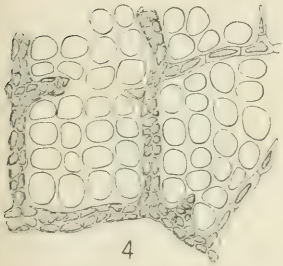
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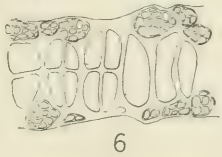
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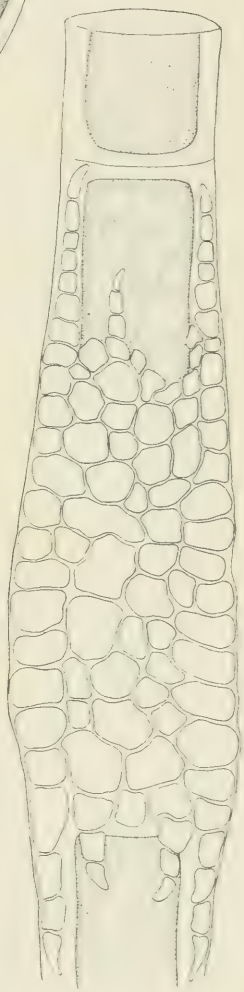
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PLATE 24

Gomontia polyrhiza (Lagerh.) B. and F.

Fig. 1. A group of three "sporangia," the two larger nearing maturity. × 175.

Gomontia habrorhiza S. and G.

Fig. 2. A young thallus. × 375.

Fig. 3. *a-e*, illustrating three forms of "sporangia."

Pseudulvella consociata S. and G.

Fig. 4. A surface view of a young thallus. × 375.

Fig. 5. A section of a mature thallus. × 375.

Fig. 6. A vertical filament near the surface of a young thallus showing branching. × 225.

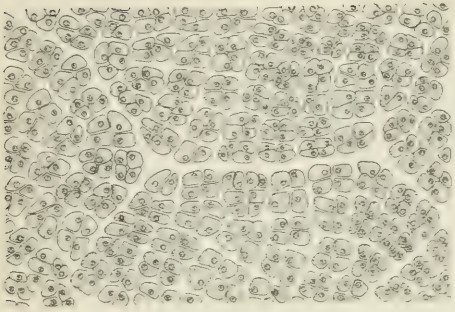
Entocladia codicola S. and G.

Fig. 7. (*a*) A young thallus, showing the method of branching of the filaments and their radiating from a center. × 125.

Fig. 7. (*b*) A mature thallus with sporangia in the center. × 125.

Prasiola delicata S. and G.

Fig. 8. A surface view showing typical arrangement of cells. × 500.



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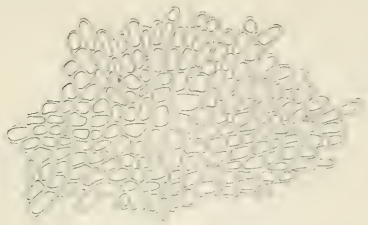

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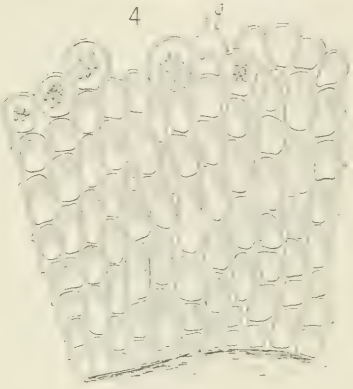

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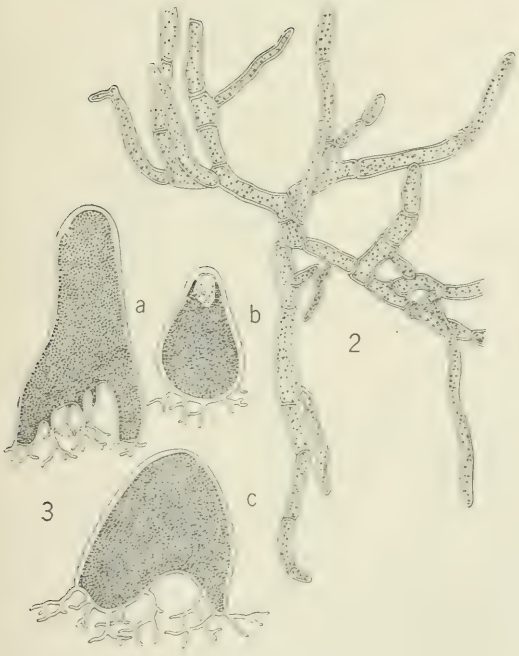
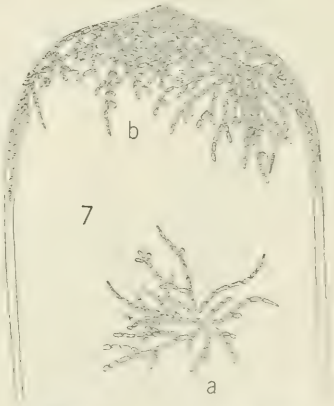




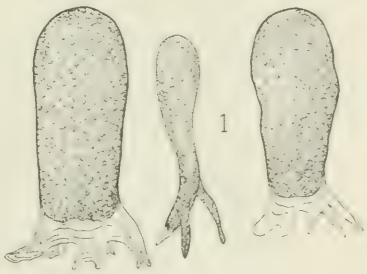


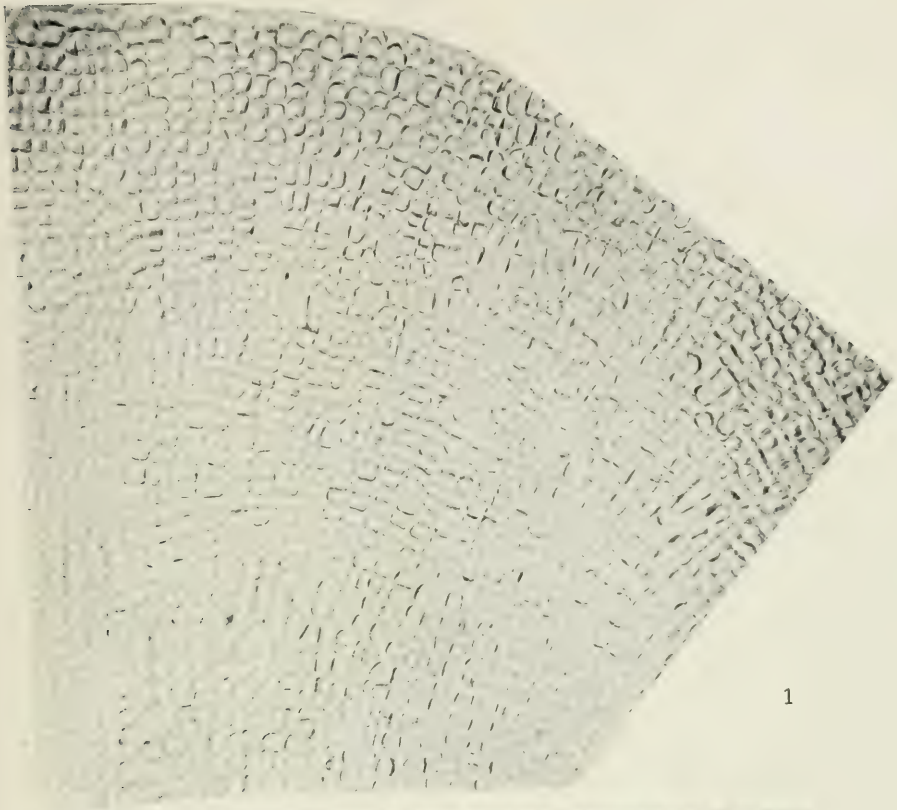
PLATE 25

Prasiola delicata S. and G.

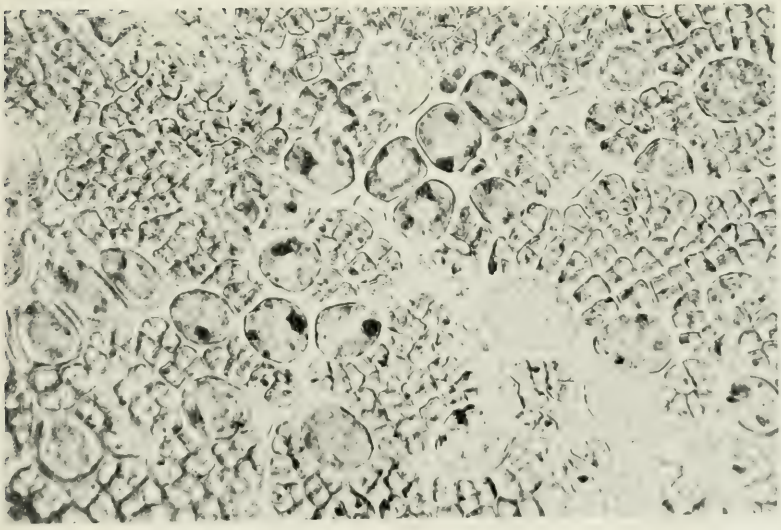
Fig. 1. A microphotograph of a marginal segment, surface view showing the arrangement of the vegetative cells. × 442.

Prasiola meridionalis S. and G.

Fig. 2. A microphotograph of a portion of the surface, showing vegetative cells and interspersed aplanospores (?). × 442.



1



2

PLATE 26

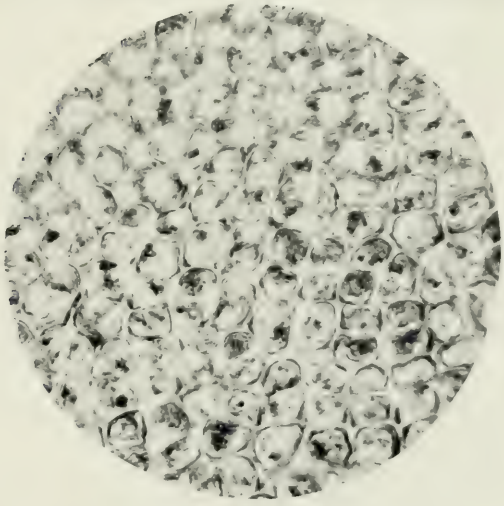
Ulva dactylifera S. and G.

Fig. 1. Photograph of a whole plant, the type specimen, with the exception of a portion of the base. × 0.75.

Ulva stenophylla S. and G.

Fig. 2. A microphotograph of a portion of the surface, showing the rounded angles and relatively thick walls of the cells. × 442.

1



2

PLATE 27

Ulva angusta S. and G.

A photograph of a group of plants, the type specimen. × 1.

PLATE 28

Ulva taeniata (Setchell) S. and G.

A photograph of a whole dried plant, showing the extreme crisped nature and the dentate margins at the base. × 0.3.

PLATE 29

Ulva stenophylla S. and G.

A photograph of the whole plant, the type specimen. × 0.3.

PLATE 30

Monostroma areolatum S. and G.

A photograph of a whole dried plant, the type specimen. × 0.5.

PLATE 31

Ulva angusta S. and G.

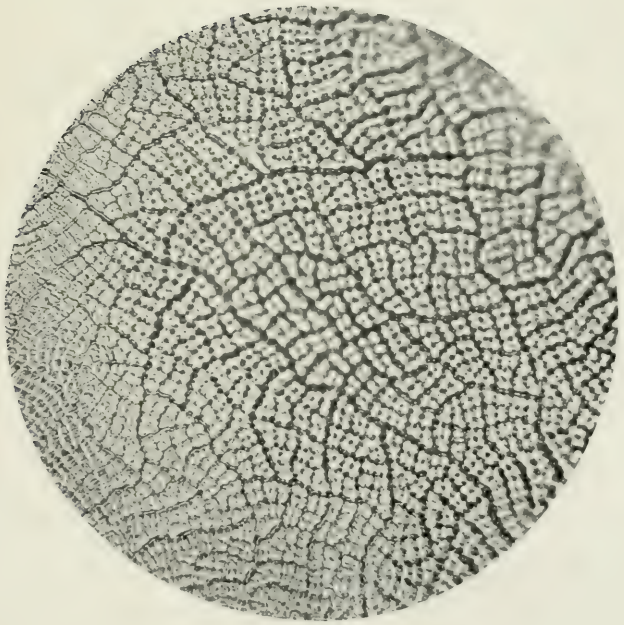
Fig. 1. A microphotograph of a part of the surface. × 442.

Monostroma areolatum S. and G.

Fig. 2. A microphotograph of a part of the surface. × 442.

The photographic work was all done by W. C. Matthews except plate 30, which was done by E. W. Merrill. All the figures of plate 21, all but figure 5 of plate 22 and figures 2, 3, 6, 7, and 8 of plate 24 were drawn by Dr. Helen M. Gilkey. All of plate 23 and figures 1, 4, and 5 of plate 24 were drawn by Miss Almeda H. Nordyke.

1



2

UNIVERSITY OF CALIFORNIA PUBLICATIONS
IN
BOTANY

Vol. 7, No. 10, pp. 325-331 December 29, 1920

PLANTAE MEXICANAE PURPUSIANAE, X

BY
TOWNSHEND STITH BRANDEGEE

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Hechtia glabra, sp. nov.

Undique glabra: scapo alto, pinnato; ramulis patentibus multifloris, inferioribus ca. 2.3 dm. longis, 2–3 cm. distantibus: foliis gradatim attenuatis margine sinuatis, spinis adscendentibus ca. 2 mm. longis praeditis, supra nitentibus subtus multo lineatis: bracteolis capsulas subtendentibus parvis: capsulis plerumque sessilibus interdum pedicellis ca. 7 mm. longis; sepalorum tubo ca. 1 mm. longo, lobis ovato-lanceolatis; petalis lanceolatis planis ca. 3 mm. longis quam sepalis duplo longioribus, basi sepalorum tubo adnatis; capsulis ca. 5 mm. longis apice stylos ca. 1.5 mm. longas recurvos gerentibus. Specimen frugiferens solum visum.

The specimens are fragmentary. The upper parts of the leaves, the only parts collected, are 5 dm. long. The panicle seems to be pinnate but may be bipinnate and is at least 5 dm. high. The attachment of the pedicellate capsules to their pedicels forms a right angle and the pedicel is closely appressed to the stem. Collected at Barranca de Panoaya, Vera Cruz. No. 8506. Type, Herb. Univ. Calif. No. 204966.

Hechtia Purpusii, sp. nov.

Foliis lanceolatis, e basi ad apicem gradatim attenuatis, basi ca. 1.8 cm. latis, usque ad 20 cm. longis, utrinque lineatim peradpresse lepidotis, pallidis, margine spinis minutissimis numerosis praeditis: scapo 5–6 dm. alto, glabro: inflorescentia tripinnatim laxe paniculata, multiflora, ramulis usque ad 13 cm. longis, pedicellis ca. 3 mm. longis, quam bracteolis lineari-lanceolatis duplo longioribus; petalis oblongis ca. 2 mm. longis, albis obtusis; ovario glabro.

This *Hechtia* differs from other species of the genus in having leaves of a thin texture margined with numerous minute spines. Collected in Barranca de Tenampa, Vera Cruz, growing on steep rocks. No. 8420. Type, Herb. Univ. Calif. No. 200824.

Ocotea pyramidata Blake, sp. nov.

Arbor grandis; ramuli nigrescentes sparse puberuli glabrati sulcati; folia oblongo-elliptica 10–18 cm. longa 4–7.5 cm. lata obtusa basi cuneato-rotundata pergamentacea supra glabra lucida laxe prominulo-reticulata subtus obscurius viridia in costa et venis 8–10 prominentibus et sparse in venulis puberula in axillis non barbata laxe prominulo-reticulata, in petiolis sparse puberulis 1–2.5 cm. longis; paniculae axillares e basi ramosae pyramidatae subsessiles 9–12 cm. longae ca. 6 cm. latae sordide puberulae; pedicelli 1–3 mm. longi puberuli; calyx 3 mm. longus subglaber, segmentis ovalibus subaequalibus rotundatis; stamina ser. I. 2.2 mm. longa glabra, filamentis antheras leviter emarginatas aequantibus, locellis introrsis per paria superpositis; stamina ser. II. similia; stamina ser. III. basi glandulis binis magnis filamenti dimidium aequantibus sessilibus donata, locellis inferioribus extrorso-lateralibus superioribus introrso-lateralibus; staminodia nulla; ovarium sterile subulatum glabrum 2 mm. longum.

This does not seem closely related to any other species known from Mexico. Type in the U. S. National Herbarium, No. 1039029, collected at Zacuapan, Vera Cruz, November, 1919; Purpus No. 8456.

Bauhinia (*Casparia*) **jucunda**, sp. nov.

Ramis glabris cinereis; foliis membranaceis glabris 5-nerviis, laete viridibus; foliolis ca. 5.5 cm. longis fere usque ad medium connatis, partibus liberis ca. 2 cm. latis, gradatim in apices obtusos ca. 4 mm. latos angustatis, apicibus ca. 6 cm. separatis; petiolis ca. 2 cm. longis; stipulis parvis cito deciduis; calycis tubo ca. 7 mm. longo, limbo deinde spathaceo; petalis linearibus tomentosis quam stamine perfecto brevioribus. Fructus deest.

Only one specimen was collected. The thin, bright green, divaricate leaves resemble those of some Passifloraе. Collected in Barranca de Panoaya, Vera Cruz, No. 8535. Type, Herb. Univ. Calif. No. 204997.

Indigofera acasonicae, sp. nov.

Fruticosa, erecta; ramis cinereis pilis brevibus; foliis erectis sessilibus vel petiolis usque ad 1 cm. longis; foliolis 3–5 cuneiformibus, 1.5–2.3 mm. longis, prope apicem ca. 5 mm. latis, apice rotundatis mucronatis, utrinque breviter pilosis pilis medifixis; stipulis ovato-lanceolatis; racemis axillaribus ca. 2 cm. longis ca. 10-floris; bracteolis parvis ovato-acuminatis quam pedicellis duplo longioribus; calycis lobis quam tubo longioribus, ovato-acuminatis; legumine tereti ca. 2.5 cm. longo, pedicello curvato deflexo, ad rachin ramosque arte adpresso.

The leaves are not spreading in the manner common to other species of the genus but stand upright close to the branches. The fruiting racemes and deflexed legumes are closely appressed to the stem and branches. Collected at Acasonica, Vera Cruz. No. 8510. Type, Herb. Univ. Calif. No. 204971.

Eriosema nigropunctatum, sp. nov.

Erectum: caulibus pubescentibus ca. 2.3 dm. altis: foliis trifoliolatis petiolis usque ad 2.3 cm. longis, foliolis lateralibus fere sessilibus, foliolo terminali petiolulo ca. 8 mm. longo; foliolis late ovatis longe acuminatis, basi truncatis, subtus dense nigropunctatis, ad venas pubescentibus, ca. 2.7 cm. longis, 2.2 cm. latis; stipulis lanceolatis ciliatis: pedunculis axillaribus paucifloris ca. 5 cm. longis; floribus ca. 6 mm. longis, stamine vexillari liberi; legumine oblongo ca. 2 cm. longo, 2-spermo paululum hirsuto apice mucronato; semine oblique transverso funiculo ad extremitam hili linearis affixo.

The ovate leaves resinose punctate beneath give to this plant the appearance of a Rhynchosia, but the position of the seed and its funicle is that of Eriosema. Collected at Palmilla near Zacuapan, Vera Cruz. No. 8386. Type, Herb. Univ. Calif. No. 200794.

Esenbeckia ovata, sp. nov.

Foliis digitatim trifoliolatis, foliolis glabris, ovatis, apice obtusissimis vel retusis, e medio in petiolum breve gradatim longe attenuatis, pellucido-punctatis, usque ad 13 cm. longis, 9 cm. latis; petiolo puberulo ca. 2 cm. longo: paniculis ca. 10 cm. longis, puberulis multifloris; petalis 5 imbricatis pellucido-punctatis; ovario 5-loculari tuberculato. Fructus deest.

The leaves are broadly ovate or obovate, very obtuse and often emarginate; from the middle they are gradually attenuate into a short petiolule. The petiolule of the usually larger terminal is longer than the short ones of the lateral leaflets. Collected at Acasonica, Vera Cruz. No. 8419. Type, Herb. Univ. Calif. No. 200823.

Euphorbia consoquitlae, sp nov.

Fruticosa, ramosa: caulibus tenuibus plus quam 6 dm. altis: foliis sparsis cito delapsis, cicatricibus pubescentibus: cymis in paniculam ca. 2 cm. longam dispositis, bracteosis, bracteis vel foliis parvis anguste ovatis vel lanceolatis usque ad 1 cm. longis; involucris paullo pubescentibus, axillaribus vel terminalibus, campanulatis; pedicellis ca.

1 cm. longis; lobis 4 oblongis, glandulis 4 planis orbicularibus, appendice iis multo longiori, ca. 2 mm. longa, apice ca. 1.5 mm. lata, basi angustiori; bracteolis inter flores masculos pubescentibus; stylis fere usque ad basin divisis; capsulae pedicellis ca. 3 mm. longis, seminibus globosis cinereis tuberculatis.

The specimens with the exception of a few leaf-like bracts of the panicle are leafless. The stems are slender and branched. Collected near Consoquitla, Vera Cruz. No. 8366. Type, Herb. Univ. Calif. No. 204969.

Jatropha longepedunculata, sp. nov.

Jatropha urens L. var. *longepedunculata* Brandg., Univ. Calif. Publ. Bot., vol. 6, p. 368.

Arborescens ad 5 m. alta, undique estimulosa: foliis latioribus quam longis usque ad 20 cm. latis, 14 cm. longis, profunde 3–5-lobatis, basi cordatis, lobis grosse dentatis; petiolis ad 20 cm. longis: pedunculis ad 23 cm. longis apice flores in cymas dichotome ramosas dispositis gerentibus; floribus femineis petalis 5 liberis, ca. 5 mm. longis, sepalis 5 parvis connatis; stylis liberis apice laceratis; floribus masculis femineis similibus, staminibus 2-verticillatis, exterioribus liberis; capsulis ca. 7 mm. longis, seminibus carunculatis.

This plant was wrongly referred to *Jatropha urens* L., from which it differs in its separated petals, its minute, cupulate, dentate calyx, lack of stinging bristles, and other characters. Collected at Barranca de Panoaya and Zacuapan, Vera Cruz. Nos. 7639, 7511, 8440.

Ayenia Purpusii, sp. nov.

Fruticulus: ramis juvenibus stellato-pubescentibus: foliis late ovatis longe acuminatis, margine serratis, basi truncatis vel subcordatis, supra glabris subtus stellato-pubescentibus usque ad 10 cm. longis, 9 cm. latis, petiolis ca. 3 cm. longis, stipulis ca. 5 mm. longis: floribus purpureis umbellatis, pedunculis ad axillas fasciculatis inaequalibus quam petiolis brevioribus; sepalis ovato-acutis ca. 1.5 mm. longis; petalorum laminis 2-partitis, lobis laciniatis, unguiculis filiformibus; ovario sessili villoso, stigmate capitato; fructu immaturo processibus linearibus ca. 2 mm. longis instructis.

The specimens appear to be branches of a bush. The young fruit is covered with linear processes and is not muricate. Collected near Zacuapan, Vera Cruz. No. 8378. Type, Herb. Univ. Calif. No. 200783.

Maba Purpusii, sp. nov.

Fructiculus? racemosus: ramis vetustis glabris brunneis, junioribus pubescentibus: foliis obovatis apice anguste obtusis basi cuneatis, margine integris minute ciliatis, utrinque fere glabris, ca. 11.5 cm. longis, 4.2 cm. latis; petiolis ca. 3 mm. longis: floribus plerumque solitariis axillaribus, pedicellis ca. 2 mm. longis; calyce extus pubescenti campanulato, ca. 1 cm. longo, usque ad medium trifido, lobis obtuse deltoideis; corolla tubulosa e calyce paululum exserta, apice 3-lobata, densissime fulvo-hirsuta; ovario hirsuto 6-loculare loculis 1-ovulatis. Fructus et flores masculi desunt.

Collected in Barranca de Panoaya, Vera Cruz. No. 8516. Type, Herb. Univ. Calif. No. 204975.

Sideroxylon campestre, sp. nov.

Arbor parva: ramis rugosis glabris: foliis ovato-oblongis utrinque glabris basi longe cuneatis, apice acutis, usque ad 18 cm. longis, 4 cm. latis, subtus venis prominulis; petiolis puberulis, ca. 2 cm. longis: floribus numerosis; pedicellis inter folios fasciculatis puberulis, ca. 1 cm. longis; segmentis calycis 6 imbricatis orbicularibus, paululum puberulis, ca. 6 mm. longis, exterioribus paulo minoribus; corolla tubulosa calycem paululum superanti, ad medium 6-lobata, lobis oblongis apice retusis, ca. 4 mm. longis; staminibus ad basin loborum affixis, filamentis longitudine antheris oblongis acutis aequalibus, ca. 3 mm. longis; staminodiis linearibus integris, staminibus aequalibus, in eadem serie alternis; ovario hirsuto 6-loculari. Baccae desunt.

The leaves with the fascicles of flowers are crowded about the ends of the branches. Collected at Zacuapan, Vera Cruz. No. 8545. Type, Herb. Univ. Calif. No. 204005.

Dictyanthus prostratus, sp. nov.

Hirsutus: caulibus pilis patentibus vel reflexis, prostrtais, basi lignosis, usque ad 7 dm. longis: foliis late cordato-ovatis acuminatis, utrinque hirsutis, ca. 2.2 cm. longis, 2 cm. latis; petiolis ca. 1 cm. longis; cymis 2-floris in una axilla, pedunculis quam petiolis multo brevioribus; calycis lobis ovato-acuminatis, ca. 3 mm. longis; corolla late campanulata atropurpurea reticulata, ca. 7 mm. longa, 6 mm. lata, lobis ovato-acuminatis. Folliculi desunt.

This species resembles closely *D. parviflorus* Hemsley, but the corona is very different. In addition to the five narrow lamellate scales adnate to the corolla there are five minute acute scales attached to the middle of the gynostegium representing an inner corona. Growing over rocks near Acasonica, Vera Cruz. No. 8411. Type, Herb. Univ. Calif. No. 200816.

Polystemma rupestre, sp. nov.

Volubile: caulibus hirsutis plus quam 8 dm. longis: foliis ovato-acuminatis, basi sinu oblongo aperto, supra hirsutulis, subtus ad venas hirsutis, usque ad 8 cm. longis, 3.3 cm. latis; petiolis ca. 2.5 cm. longis: cymis ca. 8 cm. longis, pauciforis: calyce hirsutis fere ad basin 5-lobatis, lobis lanceolatis ca. 8 mm. longis, basi ca. 2 mm. latis: corolla campanulata ca. 2 cm. longa, intus reticulata, alte lobata, lobis lanceolatis ca. 1 cm. longis; coronae squamis gynostegium affixis, quorum 5 ligulatis profunde 3-lobatis erectis, ad utrinque latus vel dorsum lobis filiformibus apice glandulam parvam gerentibus et ligulas multo superantibus; stigmate vertice plano; staminum tubo brevi; polliniis iis *P. viridiflori* similibus; folliculis juvenibus longe fusiformibus, levibus.

Collected at Barranca de Panoaya, Vera Cruz, growing on "rocky slopes." No. 8451. Type, Herb. Univ. Calif. 200855.

Pachystelma *gen. nov.* **Asclepiadacearum**

Calyx alte 5-fidus. Corolla cyathiformis 5-lobata. Coronae squamae 5, partim corollae adnatae, carnosae, tumidae, apice obtusae. Gynostegium sessile, filamentorum tubo nullo. Pollinia in quoque loculo solitaria fere pendula. Stigma vertice depressum, angulis valde prominentibus. Cymae pauciflorae in una axilla pedunculatae. Flores majusculi.

Pachystelma cordatum, sp. nov.

Volubile, frutescens: caulibus hirsutis pilis patentibus: foliis ovato-acuminatis basi cordatis sinu aperto, usque ad 7 cm. longis, 5 cm. latis, utrinque paulo breviterque hirsutis: cymis 2–3-floris, pedunculis ca. 1 cm. longis: calyce alte 5-lobata, lobis ovato-lanceolatis margine ciliatis: corolla usque ad medium 5-lobata, ca. 6 mm. alta, 8 mm. lata; coronae squamis usque ad medium corollae adnatis, carnosis, crassis, parte inferiori adnata quam parte superiori libera duplo crassa. Folliculi desunt.

The long stems twining about themselves appear to have been prostrate. The dry cup-shaped corolla is chartaceous and light colored. The scales of the corona slightly surpass the stigma, they are erect, rigid, thick, and about 1 mm. wide, at the apex are somewhat flattened and obtuse; the lower half adnate to the corolla is very much thickened. The anthers at the angles of the depressed stigmatic part are very prominent. Collected at Acasonica, Vera Cruz. No. 8008. Type, Herb. Univ. Calif. No. 204968.

Cynanchum racemosum, sp. nov.

Volubile: caulibus pubescentibus: foliis ovato-acuminatis, basi cordatis sinu aperto, lobis rotundatis, utrinque fere glabris, majoribus 6 cm. longis, 4 cm. latis; petiolis 1.3–2.3 cm. longis: floribus circa apices pedunculorum ca. 5 cm. longorum, breviter racemosis; pedicellis ca. 4 mm. longis; calycis segmentis ovato-acutis ca. 3 mm. longis corollam campanulatum superantibus; polliniis pendulis; corona membranacea cyathiformi alte 5-loba, lobis dentatis, ima basi tubi staminei affixa; stigmate vertice plano.

Collected on rocky plains near Acasonica, Vera Cruz. No. 8378. Type, Herb. Univ. Calif. No. 200783.

Solanum molestum, sp. nov.

Suffrutescens: ramis stellato-pubescentibus simul multis aculeis rectis subulatis patentibus armatis: foliis ovatis acutis, basi cordatis, margine integris vel sinuatis, plerumque solitariis, supra parce stellato-pubescentibus olivaceo-viridibus, subtus dense albo-stellato-pubescentibus, usque ad 2 dm. longis, 12 cm. latis; petiolis 3–7 cm. longis, dense stellato-pubescentibus interdum aculeos paucos gerentibus: floribus lateralibus, pedunculis unifloris 1–3 fasciculatis stellato-pubescentibus, ca. 1.5 cm. longis; calyce alte 5-lobato, lobis ovato-acutis, utrinque stellato-pubescentibus deinde reflexis, ca. 7 mm. longis; corolla calycis aequali usque ad basin 5-partitis; lobis oblongis apice obtusis, extus dense stellato-pubescentibus, intus glabris brunneis; antheris brunneis sessilibus apice poris dehiscentibus; ovario setoso; bacca densissime fulvo-setosa, diametro ca. 1.7 cm.

The fruit is covered with long yellow bristles and is more conspicuous than the colorless flowers. Collected in Barranca de Panoaya, Vera Cruz. No. 8526. Type, Herb. Univ. Calif. No. 204992.

Viguiera pauciflora, sp. nov.

Herbacea: caulibus strictis, pilosis plus quam 4 dm. altis: foliis oppositis ovato-lanceolatis basi in petiolum ca. 6 mm. longum cuneatis, ca. 3.5 cm. longis, 1 cm. latis, utrinque paululum pilosis, margine serratulis: capitulis plerumque 1 caules terminantibus, quando 2 pedunculis ca. 14 cm. longis, diametro ca. 8 mm.; phyllariis 3-seriatis induratis ovato-acuminatis appresso-pilosis; radiis luteis ca. 7 mm. longis; pappi aristis 2; squamellis fimbriatis; paleis glabris.

Stems slender, mostly bearing a single head. The specimens do not show the basal part of the plant. Collected on plains near Acasonica, Vera Cruz. No. 8375. Type, Herb. Univ. Calif. No. 200781.

Transmitted December 10, 1920.

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IN
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Vol. 7, No. 11, pp. 333-426, plates 32-49 May 16, 1922

PHYCOLOGICAL CONTRIBUTIONS II TO VI

BY

WILLIAM ALBERT SETCHELL
AND
NATHANIEL LYON GARDNER

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* Phycological Contributions I appeared as No. 9 in the present volume of this series.

II. NEW SPECIES OF MYRIONEMA

Introduction

Critical study of an extensive series of material of small filamentous species of Melanophyceae, mostly epiphytic upon larger Melanophyceae, but in part epiphytic upon other algae and upon eel-grass, has brought to light a rather surprisingly large number of little known or wholly new species and forms on the Pacific coast of North America. Among these is a series of similar organisms which we have grouped together under the genus *Myrionema*, an account of which is presented in this paper.

We are recognizing as the principal characters of this genus: (1) a monostromatic basal disk, composed of closely crowded, short celled filaments radiating from a common center, starting from a single cell, each filament having terminal growth, and branching by radial bifurcation of the terminal cell; (2) springing outward from practically all of the cells of the basal disk, except at the margin, are erect filaments all of which may be fertile, bearing either zoosporangia or gametangia, or a part of which may remain sterile; (3) the loculi of the gametangia are uniseriate.

Myrionema primarium sp. nov.

Plate 34, figure 12

Frondibus pulvinulos orbiculares, 0.5–1.25 mm. diam., formantibus; parte prostrata filamentis regulariter radiantibus arcte compactis, formante; filamentis erectis eramosis, dense stipatis, e cellula quaque filamentorum repentium oriendis; pilis veris numerosis, per medium frondis promisque sparsis; cellulis filamentorum erectorum 4–4.5μ diam., inferne quadratis, cellula apicali juvena 2–3-plo longioribus; cellulis pilorum verorum 4–5μ diam., 4–6-plo longioribus; zoosporangiis ignotis; gametangiis in filamentis repentibus sessilibus per transformatione filamenti toti quisque erecti oriendis, maxime stipatis, in medio frondibus longitudine equalibus, prope margines brevioribus, cylindricis, 55–56μ longis, 5–6μ latis, obtusis aut apice leviter attenuatis, cellula apicali acute conica.

Growing on the outer end of the young blade of *Costaria costata* in the lower littoral and the upper sublittoral belts. Oregon (Coos Bay) to central California. Type, Gardner, no. 2764 (Herb. Univ. Calif., no. 207012), mouth of Coos Bay, May.

We are considering *Myrionema primarium* to be a typical representative of a group whose members are the most primitive of the genus as considered from the standpoint of differentiation. The prostrate basal layer is composed of long, regularly radiating filaments with apical growth. Radial divisions of apical cells occur just often enough to completely occupy all of the space between each other as the plant continues to increase in diameter and in circumference. The branching is always dichotomous, and is accompanied by widening of the apical cell, and the establishment of two growing regions on opposite corners, which are subsequently separated from the remainder of the cell by a wall, thus establishing two equal branches. Beginning in the center, each cell successively toward the periphery gives rise by horizontal divisions to erect filaments of nearly equal length, the only exception or modification being that some cells give rise to long filaments, the so-called true hairs, with the meristem at the base, and the outer cells long and colorless. All other erect filaments are transformed into gametangia. Only the cells of the basal filaments remain sterile, or probably a few short erect filaments at the periphery of the frond may never come to maturity. Thus starting with a single cell, the maximum of reproductive cells arises in this group. Starting with such forms the course of evolution seems to have been in the direction of the sterilization of tissue.

Myrionema primarium f. **acuminatum** forma nov.

Plate 32, figure 9

Frondibus microscopicis, inter algas parvas alteras crescentibus; filamentis erectis pro parte sterilibus, 80–100μ longis, cellulis leviter doliiformibus; gametangiis 4–5μ diam., acuminatis, pro parte brevipedicellatis.

Growing on *Macrocystis pyrifera*. Carmel Bay, Monterey County, California. Type, Gardner, no. 3110*b* (Herb. Univ. Calif., no. 207014), December.

There is but a slight difference between *M. primarium* and forma *acuminatum*. It is worthy of note that many gametangia in the center of the thallus are short pedicellate (plate 32, fig. 9), and that a few, about one in twenty-five, of the erect filaments continue to grow, attaining a length of two to three times as long as the gametangia.

Myrionema minutissimum sp. nov.

Plate 34, figures 1–3

Frondibus pulvinulos inconspicuos, 0.75–1.5 mm. diam., formantibus; parte prostrata filamentis dense compactis, regulariter radiantibus composita; filamentis erectis dense stipatis, cylindricis, omnibus fructiferis; pilis veris ignotis; cellulis filamentorum repentium 4μ diam., in centro frondis, quadratis, ad margines leviter longioribus quam latis; cellulis filamentorum erectorum similibus iis repentium; zoosporangiis et "ascocystis" ignotis; gametangiis pedicellis 4–8-cellulis compositis suffultis, cylindricis, dense stipatis, 34–40μ longis, 4–4.5μ latis.

Growing on the cysts of *Egregia Menziesii*. Cast ashore near the "Cliff House," San Francisco, California. Type, Gardner, no. 4123*b* (Herb. Univ. Calif., no. 207020), November.

Myrionema minutissimum may be distinguished by the absence of sterile erect filaments and hairs, and by the small sized, very densely crowded pedicellate gametangia. Thus far no "ascocysts" nor zoosporangia have been observed. In its phylogenetic relationship it would seem to stand equally close to *M. corunnae* and *M. foecundum*, differing from each, however, in details of measurements. The erect filaments are of the same diameter at their bases as the length of the cells in the creeping filaments. Since the lower part of each remains sterile, it gives the mass of cells the appearance of being parenchymatous.

Myrionema foecundum f. **simplicissimum** forma nov.

Plate 33, figures 9, 10

Frondibus pulvinulos orbiculares, 0.5–1.5 mm. diam. formantibus; parte prostrata filamentis regulariter radiantibus et arcte adhaerantibus augmentatione ramificationeque apicali composita; filamentis erectis omnibus fructiferis; pilis veris ignotis; cellulis filamentorum repentium 3–4.5μ diam., medio quadratis, prope marginem 2-plo longioribus; zoosporangiis ignotis; "ascocystis" raris usque ad numerosis, clavatis 28–34μ altis; gametangiis transformatione filamenti omnis quisque erectiis marginis frondis exceptis oriendis, 30–40μ altis, 7–9μ latis.

Growing on the sporophylls of *Nereocystis Luetkeana*. Puget Sound, Washington, to central California. Type, Gardner, no. 4316 (Herb. Univ. Calif., no. 207022), Moss Beach, San Mateo County, California, July.

We have not seen either the type or any other authentic material of *Phycocelis foecunda* Stroemfelt. Neither have we any authentic

measurements of the original. De-Toni (1895, p. 582) gives 35μ to 70μ as the height and 7μ to 12μ as the width of the gametangia. In height of gametangia our form approximates to forma *seriata* Reinke (1889, p. 46), but has no true hairs so far as we have ever been able to observe from the examination of many specimens from different localities.

At times the individuals are very numerous on the host, so much so as to interfere with each other's growth. In one collection (Gardner, no. 4651) they are completely confluent over several square inches, and the outline of the individuals can be detected only by staining and by microscopic examination.

Myrionema foecundum f. **subulatum** forma nov.

Plate 33, figures 1–3

Filamentis basalibus per ramulos numerosos, subulatos, 2–4 cellulis compositos, inter cellulas hospitis penetrantes annectis; zoosporangiis, "ascocystis" et pilis veris ignotis.

Growing on the sporophylls of *Nereocystis Luetkeana*. Near the "Cliff House," San Francisco, California. Type, Gardner, no. 4651 (Herb. Univ. Calif., no. 207028), November.

Forma *subulatum* is very similar to forma *simplicissimum*. The gametangia average slightly larger, and are usually more blunt. There are no so-called "ascocysts" present. The chief distinction is the presence in this form of numerous awl-shaped rhizoids, found in no other form of the species, so far as we have been able to ascertain.

Myrionema foecundum f. **ramulosum** forma nov.

Plate 33, figure 8

Frondibus pulvinulos parvos, orbiculares, 1–3 mm. diam. formantibus; filamentis erectis superne sparse ramosis, 55–65μ longis; cellulis filamentorum erectorum 5.5–6.5μ diam. quadratis, cellulis terminalibus frequenter 2–3-plo longioribus quam latis; zoosporangiis, "ascocystiis," et pilis veris ignotis; filamentis erectis omnibus in gametangia transformatis.

Growing on the pneumatocysts of *Nereocystis Luetkeana*. Friday Harbor, San Juan Island, Washington. Type, Gardner, no. 4065 (Herb. Univ. Calif., no. 207018), August.

This form of *M. foecundum* differs from the other forms of the species in having secund "proliferations" near to the outer ends of many of the gametangia.

Myrionema foecundum f. **divergens** forma nov.

Plate 34, figures 8, 9

Frondibus pulvinulos orbiculares, 1.5–3.5 mm. diam. formantibus; parte basali filamentis dense compactis, conjunctim et ad superficiem hospitis arcte adhaerente; filamentis sterilibus erectis exigiis, eramosis, obtusis, promisque inter gametangiis sparsis, 300–400μ longis; pilis veris deuntibus; "ascocystis" numerosis, inter, et brevioribus quam, gametangiis, sparsis, cylindricis usque ad clavatis; cellulis filamentorum repentium 5–6μ diam., 1.5–2-plo longioribus; cellulis filamentorum erectorum 8–9μ diam., 1.5–3-plo longioribus, cylindricis, non constrictis, zoosporangiis ignotis; gametangiis forma variabilibus, cylindricis, cylindro-conicis usque ad fusiformibus, 50–60μ longis, 7.5–8.5μ latis; loculis 1–2-seriatis.

Growing on the sporophylls of *Nereocystis Luetkeana*. Pacific Grove, California. Type, Gardner, no. 4511 (Herb. Univ. Calif., no. 207024), December.

This form of *M. foecundum* manifests some slight differentiations not present in any other form of the species. Scattered promiscuously over the frond are erect filaments two to three times as long as the gametangia. The "ascocysts" are abundant. Some irregularities are also shown in the creeping filaments. Typically the branching seems to take place by the splitting of the apical cell, but it seems that frequently one of the dichotomy fails to develop till later, producing the appearance of lateral branching. There is also an occasional oblique or longitudinal division of a cell of the creeping filaments perpendicular to the host.

Myrionema foecundum f. majus forma nov.

Plate 32, figure 7

Frondibus pulvinulos orbiculares, 1–2 mm. diam., superficie superiore convexa; parte prostrata filamentis arcte adhaerantibus, regulariter radiantibus composita; filamentis erectis dense stipatis, simplicibus, cellulis cylindricis, 5–7μ diam.; pilis veris sparsis, per frondem promiscue distributis, basim meristematicis, vaginatis, 400–500μ longis, cellulis 6μ diam. apice, 5–8-plo longioribus; "ascocystis" in filamentis prostratis sessilibus, cylindricis, apice leviter distentis, 45–55μ longis, 8–12μ latis, nunc in fronde tota sparsis nunc in gregibus isolatis; zoosporangiis ignotis; gametangiis in filamentis basalibus sessilibus, cylindricis, 60–80μ longis, 6–8μ latis, per transformationem quisque toti filamenti oriendis, dissepimentis horizontalibus aut obliquis.

Growing on *Laminaria ephemera* Setchell. Port Renfrew, Vancouver Island, Neah Bay, Puget Sound (Tacoma) and central California (Carmel Bay). Type, Gardner, no. 2910 (Herb. Univ. Calif., no. 207013), Carmel Bay, California, May.

This small epiphyte seems to be restricted in its habitat to the above named host. The only known localities in which the host has been observed are those mentioned above. The material from each locality is richly infested by this epiphyte. The host, richly infested, was distributed by Miss Josephine Tilden in her American Algae (Exsicc.), no. 609, under *Renfrewia parvula* Griggs.

It seems very closely related to *Myrionema foecundum* f. *simplicissimum*. The differences are in the larger measurements of all of the parts, the presence of numerous, larger, so-called ascocysts, occurring in groups (see plate 32, figure 7), or scattered among the gametangia, in the presence of well developed hairs, and in the more convex upper surface of the mass of erect filaments.

Myrionema corunnae f. **uniforme** forma nov.

Plate 33, figures 4, 5

Frondibus pulvinulos irregulares 0.5–1.5 mm. diam. formantibus; filamentis repentibus stratum compactum augmentatione peripherica efficientibus; pilis veris deuntibus; filamentis erectis eramosis, apice leviter attenuatis, 80–100μ (usque ad 120μ) altis; cellulis filamentorum erectorum 4.5–5.5μ diam., 1–1.5-plo longioribus; "ascocystis" sparsis, clavatis; gametangiis stratum solidum compactum, ordine palorum, centro altitudine aequalibus, ad margines gradatim diminuendis, plerumque sessilibus, nunc pedicellis 1–3 cellulis compositis suffultis, 80–100μ altis, 6–6.5μ latis; loculis uniseriatis.

Growing on the blades of *Costaria costata*, *Liminaria Sinclairii*, and *Alaria marginata*. Central California (Moss Beach in San Mateo County, Fort Point in San Francisco). Type, Gardner, no. 4473 (Herb. Univ. Calif., no. 207023), San Francisco, July.

Forma *uniforme* differs from the species as described and figured by Sauvageau (1897, pp. 77–82, repr., figs. 14 A–F) in having no hair filaments, in having no branched gametangia, in having "ascocysts," and in having slightly different dimensions.

There are some differences in the size of the plants we have found growing on different hosts in central California. The plants chosen as the type of the form grow on the blades of *Alaria marginata* at Fort Point, San Francisco. Very generally, this species of *Alaria* has delicate grooves obliquely radiating from the midrib to the margin. The presence of these grooves is often accentuated by the growth of this minute *Myrionema*, usually so numerous as to be confluent, so that the individuals cannot be detected except by microscopic examination.

Myrionema corunnae f. **angulatum** forma nov.

Plate 33, figures 6, 7

Frondibus pulvinulos microscopicos linea exteriore irregularibus, in hopites inter algas alteras parvas, formantibus; filamentis repentibus sub conditiones augmentationis liberae radiantibus; filamentis erectis eramosis, dense stipatis, 130–140μ longis; pilis veris deuntibus; cellulis filamentorum repentium 4–4.5μ diam., plerumque quadratis; cellulis filamentorum erectorum cylindricis, 4–4.5μ diam., 1.5–3-plo longioribus; zoosporangiis et "ascocystis" ignotis; gametangiis cylindricis, apice leviter attenuatis, in pedicellis cellulis 6–10 compositis suffultis, 35–45μ (usque ad 60μ) longis, 4–6.5μ latis, septorum multis obliquis.

Growing on the cysts of *Egregia Menziesii*. Cast ashore near the "Cliff House," San Francisco, California. Type, Gardner, no. 3471*b* (Herb. Univ. Calif., no. 207015), August.

This form is to be distinguished from the species as described by Sauvageau (1897, pp. 77–82, repr.) by the absence of hairs, the presence of sterile erect filaments, the gametangia mostly on longer pedicels and by the very small size of the loculi, often produced by perpendicular and slanting walls. In part, the gametangia seem pluriseriate, caused by the division of some of the original cells into small, angular loculi.

Myrionema corunnae f. **sterile** forma nov.

Plate 33, figures 13–15

Frondibus pulvinulos orbiculares 1.5–3 mm. diam. formantibus; filamentis erectis rectis, simplicibus, cylindricis, obtusis, 55–65μ longis; pilis veris et "ascocystiis" deuntibus; gametangiis cylindricis, obtusis, in pedicellis cellulis 3–5 compositis suffultis, raro sessilibus, 55–65μ longis, 4.5–5.5μ latis; gametangiis et filamentis erectis sterilibus e centro ad margines frondis longitudine regulariter gradatimque diminuendis.

Growing on the pneumatocysts of *Nereocystis Luetkeana*. Cast ashore, Carmel Bay, Monterey County, California. Type, Gardner, no. 4557 (Herb. Univ. Calif., no. 207027), December.

This form is to be distinguished from the species as described by Sauvageau (1897, pp. 77–82, repr.) by the presence of numerous sterile erect filaments interspersed among the gametangia, about one-fourth to one-fifth as many as the gametangia, in the absence of hairs, and in the very gradual diminution in the length of the sterile filaments and the gametangia from the center to the circumference of the fronds. The sterile erect filaments are of the same length as the gametangia.

Myrionema balticum f. **pedicellatum** forma nov.

Plate 33, figures 11, 12

Frondibus pulvinulos microscopicos 150–400μ (usque ad 800μ) diam., linea exteriore maxime irregulares formantibus; filamentis erectis pro parte brevi piliferis, 140–160μ longis; pilis veris ignotis; zoosporangiis(?) anguste clavatis, in filamentis repentibus sessilibus aut in filamentis erectis terminalibus; gametangiis in pedicellis cellulis 10–15μ compositis suffultis terminalibus aut sessilibus, usque ad 150μ longis.

Growing on the outer ends of the leaves of *Phyllospadix* sp. Point Carmel, Monterey County, California. Type, Setchell, no. 5417 (Herb. Univ. Calif., no. 207030), June.

This form differs from the species in the absence of hairs, in having a few very short-piliferous, vegetative filaments, and in having the gametangia on long pedicels.

In this form, as in many others, the correct interpretation of the zoosporangia mentioned above in the diagnosis is an open question. They are filled with dense cell contents, and, although none have been observed to produce zoospores, they appear as though they might later. Whatever their nature may finally prove to be, they represent another character in which this form differs from the species. Reinke neither figures nor describes them in *Ascocyclus balticus*. They appear on the same individuals with the gametangia or on different individuals.

Myrionema balticum f. **californicum** forma nov.

Frondibus pulvinulos microscopicos, 0.5–0.75 mm. diam.; parte prostrata filamentis relative rectis, regulariter radiantibus composita; filamentis erectis simplicibus, et superne et inferne leviter attenuatis, obtusis, 75–125μ longis; pilis veris 0.5–1 mm. longis; cellulis filamentorum prostratorum 6–7μ diam., 1–1.5-plo longioribus; cellulis filamentorum erectorum 7.5–10μ diam., quadratis; cellulis pilorum verorum 4–5.5μ diam., superne 6–10-plo. longioribus, basi 3–5-plo longioribus, sed cellulis paucis basim superne remotis quadratis; chromatophoris taeniatis irregulariter interruptis compositis; zoosporangiis ignotis; gametangiis pedicellis 1–3 cellulis compositis suffultis, aut e filamentis repentibus aut e basibus filamentorum erectorum lateralibus oriendis, cylindricis, 90–130μ longis, 7–9μ latis.

Growing on the outer ends of the leaves of *Phyllospadix* sp. Point Carmel, Monterey County, California. Type, Setchell, no. 5439 (Herb. Univ. Calif., no. 207031), June.

We have no authentic measurements of *Ascocyclus balticus* Reinke. He does not mention the size of the gametangia either in the Atlas

(1889, pl. 16, figs. 1–4), where he first describes and figures it, or in the Algenflora (1889*a*, p. 45) where he describes it again. Foslie (1894, p. 17, repr.) made the combination *Myrionema* (*Phycocelis*) *balticum*, but he gave no measurements for any of its parts. De-Toni (1895, p. 581) lists the plant as *Phycocelis(?) baltica* (Reinke) Foslie, but gives no additional information concerning the size of the gametangia. Kylin (1907, p. 35) lists a plant under *Myrionema balticum* (Rke.) Fosl. which he found growing on *Delesseria sanguinea* at 15 M. depth. He states that the assimilation filaments are 100–125μ long and 4–6μ broad, but gives no measurements for the gametangia.

The plant which we have diagnosed here is doubtless very closely related to Reinke's *Ascocyclus balticus*. It may be a distinct species, but we are listing it as a form of *balticus* until we can obtain more knowledge of its variation, and more authentic information concerning the type material of *balticus*. The particular distinguishing character is the very frequent occurrence of lateral gametangia arising very close to the base of the vegetative filaments.

Myrionema globosum f. **affine** forma nov.

Plate 33, figure 16

Frondibus microscopicis, 200–300μ diam., linea exteriore irregularibus, algis alteris parvis immixtis; filamentis prostratis multo distortis, libere ramosis; filamentis erectis fasciculato-ramosis, 100–140μ longis, superne attenuatis, pro parte piliferis; pilis veris 300–400μ longis; cellulis filamentorum prostratorum 4–6μ diam., forma variabilibus; cellulis filamentorum erectorum cylindricis, 4–5μ diam.; zoosporangiis ignotis; gametangiis cylindricis, 35–45μ longis, 4–4.5μ latis, in filamentis erectis sessilibus lateralibusque aut raro terminalibus; loculis uniseriatis.

Growing on the leaves of eel-grass. Sitka, Alaska, to central California (Point Carmel, Monterey County). Type, Setchell, no. 5439*a* (Herb. Univ. Calif., no. 207032), Point Carmel, June.

We have no measurements in detail for the parts of *Myrionema globosum*, this seemingly distinct species. Reinke (1889a, p. 46) states that the plants are one-half to one millimeter in diameter. Our plants seem much smaller, in general. It is difficult to make out the size on account of their being so intimately intermixed with other small algae. This is the case in both collections of plants which we have examined, one from Sitka, Alaska, and the other from Point Carmel, California. We are placing it as a form of *M. globosum* (Reinke) Foslie, awaiting knowledge of further details concerning the type.

Myrionema compsonematoides sp. nov.

Plate 34, figure 10

Frondibus pulvinulos microscopicos linea exteriore irregulares, 200–400μ diam. formantibus; parte prostrata filamentis distortis composita; filamentis erectis cylindricis, simplicibus 70–80μ altis, pilis veris ignotis; cellulis filamentorum repentium forma magnitudineque aliquantum irregularibus, 4–6μ diam.; cellulis filamentorum erectorum cylindricis, 5–7μ diam., quadratis; "ascocystis" sparses, terminalibus aut prope basim filamentorum erectorum lateralibus; gametangiis fusiformibus usque ad clavatis, sessilibus aut brevi-pedicellatis, 50–65μ longis, 7–10μ latis; loculis inferne uniseriatis, superne biseriatis.

Growing on the blade of *Laminaria complanata*. Friday Harbor, Washington. Type, Gardner, no. 4118 (Herb. Univ. Calif., no. 207019), August.

Myrionema compsonematoides seems to be a modification of *M. foecundum*. There is a slight sterilization of tissue in that a few of the erect filaments remain sterile and develop slightly beyond the gametangia, and in that a part of the gametangia are pedicellate. It seems to tend toward *Compsonema* in these respects, and in having biseriate gametangia in part.

Myrionema hecatonematoides sp. nov.

Plate 34, figure 11

Frondibus pulvinulos tenues dilute fuscos, linea exteriore irregulares, usque ad 6 mm. diam. formantibus; parte prostrata filamentis distortis, irregulariter radiantibus composita, plerumque monostromatica, pro parte distromatica, inferne ramulos radiciformes penetrantes, paxilliformes, paucos emittente; filamentis erectis simplicibus, cylindricis, 240–260μ longis; pilis veris deuntibus; cellulis filamentorum erectorum 6.5–7.5μ diam., 2–3-plo longioribus; zoosporangiis ignotis; gametangiis sessilibus aut in pedicellis 1–2-cellulis compositis e filamentis repentibus oriundis suffultis, cylindricis usque ad fusiformibus, 45–55μ longis, 7–8.5μ latis; loculis plerumque uniseriatis, in parte latiore gametangiorum biseriatis.

Growing on the pneumatocysts of *Nereocystis Luetkeana*. Pacific Grove, California. Type, Gardner, no. 4533 (Herb. Univ. Calif., no. 207025), December.

As indicated by the partial distromatic base, the slight tendency to biseriate loculi in the gametangia and the sterilization of a part of the erect filaments, this species of *Myrionema* seems to be differentiating in the direction of the genus *Hecatonema*. We are retaining it in the genus *Myrionema* because of a preponderance in number of uniseriate loculi and monostromatic filaments in the prostrate portion.

Myrionema attenuatum sp. nov.

Plate 34, figures 6, 7

Frondibus strata microscopica plus minusve confluentia in superficie hospitis formantibus; parte prostrata filamentis, regulariter radiantibus composita; filamentis erectis simplicibus superne basimque leviter attenuatis, 180–220μ longis, pilis veris deuntibus; cellulis filamentorum repentium 4.5–5.5μ diam., proxime quadratis; cellulis filamentorum erectorum 6–7μ diam., longitudine variabilibus; zoosporangiis ignotis; gametangiis sparsis, cylindricis usque ad leviter fusiformibus in pedicellis longioribus aut brevioribus, 30–45μ longis, 4.5–6μ latis.

Growing on the stipes of *Macrocystis pyrifera*, *Laminaria Farlowii*, and on the sterile base of *Gigartina radula* f. Carmel Bay, Monterey County, California. Type, Gardner, no. 4685*a* (Herb. Univ. Calif., no. 207029), December.

It seems that sterilization has proceeded in this species of *Myrionema* until about two-thirds of the erect filaments no longer produce gametangia, and these filaments are several times longer than the gametangia. The cells are slightly doliiform in some collections.

Myrionema attenuatum f. doliiforme forma nov.

Plate 34, figures 4, 5

Frondibus flocculos parvos, irregulares, inter algas alteras epiphyticas formantibus; filamentis erectis usque ad 275μ longis; cellulis filamentorum erectorum quadratis usque ad 3-plo longioribus quam latis haud dubie doliiformibus; gametangiis nunc parvis et in filamentis longis erectis terminalibus nunc ut in forma species typica.

Growing on the stipe of *Macrocystis pyrifera*. Carmel Bay, Monterey County, California. Type, Gardner, no. 4540*a* (Herb. Univ. Calif., no. 207026), December.

The chief distinction between this form and the species, *M. attenuatum*, is the decided doliiform character of the erect filaments. Small terminal gametangia appear very frequently on the long, erect filaments.

Myrionema phyllophilum sp. nov.

Plate 32, figures 1–5

Frondibus pulvinulos plus minusve orbiculares, 400–800μ diam. formantibus; parte repente filamentis rectis e centro radiantibus, dense compactis composita; filamentis erectis simplicibus, cylindricis, basim constrictis, 110–130μ longis, pro parte superne leviter attenuatis piliferisque; pilis veris inter filamenta gametangiaque promiscue

sparsis; cellulis filamentorum repentium cylindricis, 4–5μ diam., 2–4-plo longioribus; cellulis filamentorum erectorum 8–9μ diam., quadratis usque ad 2.5-plo longioribus; cellulis pilorum verorum basim quadratis, superne 5–6μ diam. et usque ad 20-plo longioribus; zoosporangiis(?) late clavatis, sessilibus aut in pedicellis longioribus aut brevibus suffultis, 50–70μ longis, 14–18μ superne latis; gametangiis cylindricis, plerumque in pedicellis 1–2-cellulis compositis suffultis in filamentis repentibus aut rariore in basi filamentorum erectorum lateralibus, obtusis, 90–130μ longis, 9–11μ latis; loculis uniseriatis.

Growing on the outer ends of the blades of eel-grass, in the lower littoral and upper sublittoral belts. Sitka, Alaska. Type, Gardner, no. 3969 (Herb. Univ. Calif., no. 207017), July.

In this species about one-third of the erect filaments remain sterile, and extend beyond the gametangia. The cells in the creeping filaments are relatively long. The filaments are closely crowded, but distinct and readily separable. All the erect filaments are abruptly narrowed at the base. On account of the long creeping cells, the erect filaments are very much less crowded than is usually the case in most *Myrionemas*. The erect filaments do not arise successively toward the margin of the nearly mature plants. Cells here and there develop an erect filament to the length of several cells before the intervening cells show signs of farther growth. The gametangia are typical of the genus, with uniseriate loculi and with mostly horizontal, cross cell-walls. The zoosporangia(?) are fairly abundant, and are either with the gametangia on the same individual or on separate individuals. We question these structures as being functional since none of them has been observed to produce zoospores. They have the appearance of being abortive organs, either zoosporangia or gametangia, more likely the latter, and are probably like the organs observed by Magnus which induced him to establish the genus *Ascocyclus*.

Myrioenma setiferum sp. nov.

Plate 32, figure 8

Frondibus flocculos aut pulvinulos parvos, densos, irregulares, 0.5–0.75 mm. diam. formantibus; parte prostrata filamentis regulariter radiantibus, dense compactis, cellulis 4–5μ diam., prope margines 1.5–3-plo longioribus composita; pilis veris ignotis; filamentis erectis numerosis, simplicibus, apice leviter attenuatis, longe-piliferis, 700–800μ longis; cellulis filamentorum erectorum cylindricis, 4–5μ diam., 2–3-plo longioribus; zoosporangiis late clavatis, 80–90μ longis, 18–24μ latis; gametangiis cylindricis, 150–200μ longis, 7–8.5μ latis, sessilibus aut in pedicellis curtis in filamentis erectis aut raro in filamentis repentibus suffultis; loculis uniseriatis.

Growing on the outer ends of the leaves of eel-grass, in company with other small algae, in the lower littoral belt. Sitka, Alaska. Type, Gardner, no. 3968*c* (Herb. Univ. Calif., no. 207016), July.

Myrionema setiferum is undoubtedly very closely related to *M. phyllophilum* on the one hand, and to *M. foecundum* f. *californicum* on the other. From the former, it differs in having longer and narrower erect filaments with longer cells and in having much longer and narrower gametangia which are more frequently borne laterally on the erect filaments, and often fasciculately branched from a short pedicel. From the latter, it differs in having functional zoosporangia, one of the few instances in which we have actually seen the undoubted zoospores, in having longer and setiferous erect filaments, and longer and slightly narrower gametangia.

Myrionema obscurum sp. nov.

Plate 32, figure 6

Frondibus microscopicis, supra superficiem hospitis irregulariter dispersis; filamentis repentibus multo ramosis, maxime compactis et contortis, stratum pseudo-parenchymaticum formantibus; filamentis erectis sparsis, simplicibus, 40–70μ altis; pilis veris ignotis; cellulis filamentorum repentium forma magnitudineque maxime irregularibus, 4.5–10μ diam., cellulis filamentorum erectorum cylindricis, 6.5–7.5μ diam., exacte aut fere quadratis; zoosporangiis numerisissimis, in filamentis repentibus, sessilibus, ovoideis usque ad late clavatis, 45–65μ longis, 18–30μ latis; gametangiis ignotis.

Growing on the blade of *Costaria costata*. Moss Beach, San Mateo County, California. Type, Gardner, no. 4315 (Herb. Univ. Calif., no. 207021), July.

Myrionema obscurum seems decidedly distinct from all other species of the genus. It seems to be a near relative of *M. strangulans* Grev. The basal layer is very compact, and adheres very firmly to the host, following closely the irregularities on its surface. We are unable to make out whether or not the epiphyte causes the death of the cells of the host, which seems to be quite frequent in all of the plants we have observed. The creeping filaments push among the dead cells of the host at times. The zoosporangia are numerous and all sessile.

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PLATE 32

Myrionema phyllophilum S. and G.

Fig. 1. A single creeping filament near the margin of a frond showing zoosporangia(?) and young erect filaments. × 250.

Fig. 2. The same as figure 1, but illustrating the gametangia. × 250.

Fig. 3. A fragment from the center of a mature plant showing a true hair, mature erect filaments with terminal hairs, and gametangia. × 125.

Fig. 4. The same as figure 3, but illustrating sessile zoosporangia(?). × 125.

Fig. 5. A segment of the basal portion showing the compact nature of the radiating filaments. × 125.

Myrionema obscurum S. and G.

Fig. 6. A few fragments of typical plants. × 125.

Myrionema foecundum f. *majus* S. and G.

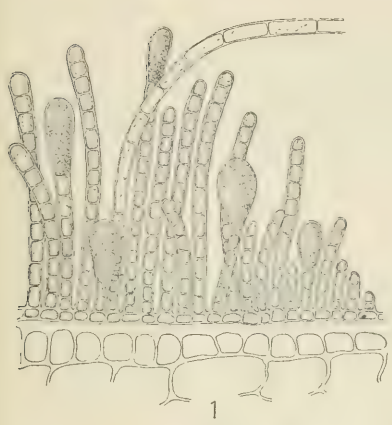
Fig. 7. A terminal part of a creeping filament showing a group of so-called ascocysts, true hairs, and typical gametangia. × 250.

Myrionema setiferum S. and G.

Fig. 8. A fragment of a typical plant. × 125.

Myrionema primarium f. *acuminatum* S. and G.

Fig. 9. Fragments taken from different parts of a plant. × 250.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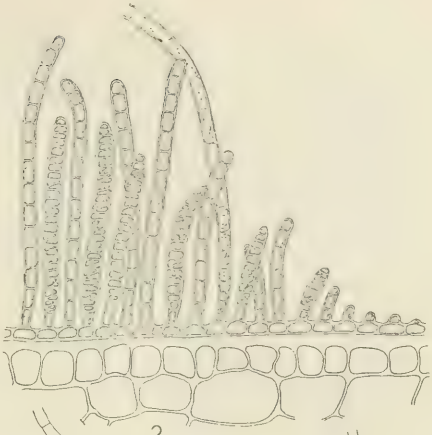
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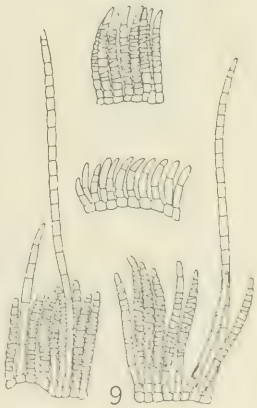
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PLATE 33

Myrionema foecundum f. *subulatum* S. and G.

Fig. 1. A section through a plant and its host perpendicular to the surface, taken near the margin. × 125.

Fig. 2. Same as figure 1. × 250.

Fig. 3. A segment of the base at the margin on the surface of the host. × 125.

Myrionema corunnae f. *uniforme* S. and G.

Fig. 4. Three fragments of plants showing the base and typical gametangia. × 250.

Fig. 5. Segments of the base, diagrammatic.

Myrionema corunnae f. *angulatum* S. and G.

Fig. 6. A part of a frond taken near the center of the frond. × 250.

Fig. 7. A part of the frond taken near the circumference of the frond. × 250.

Myrionema foecundum f. *ramulosum* S. and G.

Fig. 8. Two fragments of fronds showing the base and typical gametangia. × 125.

Myrionema foecundum f. *simplicissimum* S. and G.

Fig. 9. A section through a frond near its margin, and its host perpendicular to the surface showing the base, the sessile gametangia and the so-called ascocysts. × 125.

Fig. 10. A section showing the "ascocysts" grouped. × 250.

Myrionema balticum f. *pedicellatum* S. and G.

Fig. 11. A group of typical gametangia and erect filaments from the basal layer. × 125.

Fig. 12. Same as figure 10 with zoosporangia(?). × 125.

Myrionema corunnae f. *sterile* S. and G.

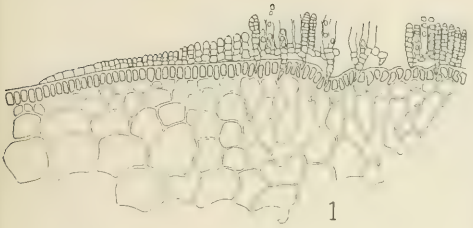
Fig. 13. A diagrammatic section to show the gradual diminution in the length of the erect filaments from the center to the circumference of the frond.

Fig. 14. A section at the margin of the frond. × 250.

Fig. 15. A section through the center of the frond showing mature gametangia and interspersed sterile filaments. × 250.

Myrionema globosum f. *affine* S. and G.

Fig. 16. A fragment of a typical plant. × 125.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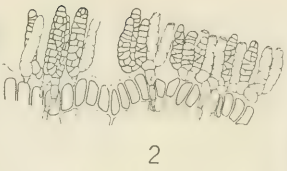
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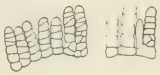

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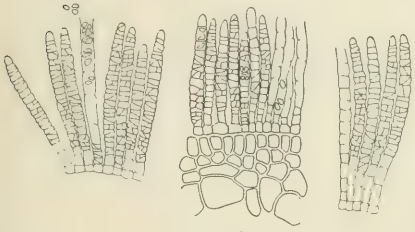
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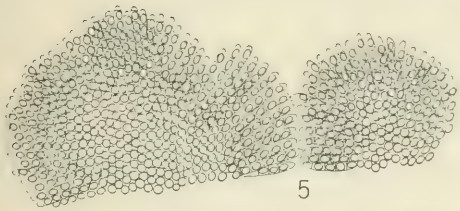
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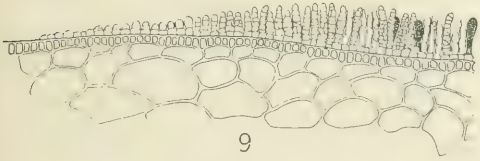
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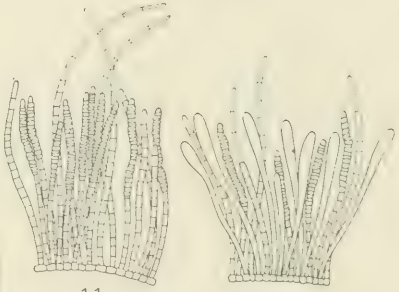
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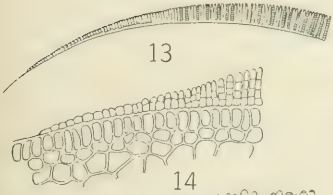
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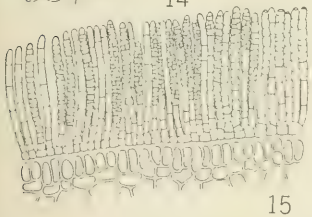
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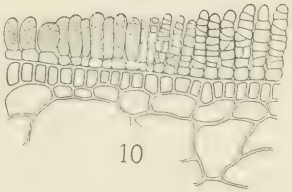
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PLATE 34

Myroinema minutissimum S. and G.

Fig. 1. Two groups of gametangia, the left, younger, and the right, older. × 125.

Fig. 2. A segment of the base showing the typical splitting of the terminal cells. × 250.

Fig. 3. Small groups of gametangia showing different lengths of pedicels. × 250.

Myrionema attenuatum f. *doliiformum* S. and G.

Fig. 4. A fragment showing relatively large erect sterile filaments and relatively small and few gametangia. × 250.

Fig. 5. A fragment showing the opposite condition to that of figure 4. × 250.

Myrionema attenuatum S. and G.

Fig. 6. A fragment taken near the margin of the frond. × 250.

Fig. 7. A fragment taken near the center of the frond. × 250.

Myrionema foecundum f. *divergens* S. and G.

Fig. 8. Sections taken from four different places in the frond. × 125.

Fig. 9. A segment of the base at the margin of the frond. × 250.

Myrionema compsonematoides S. and G.

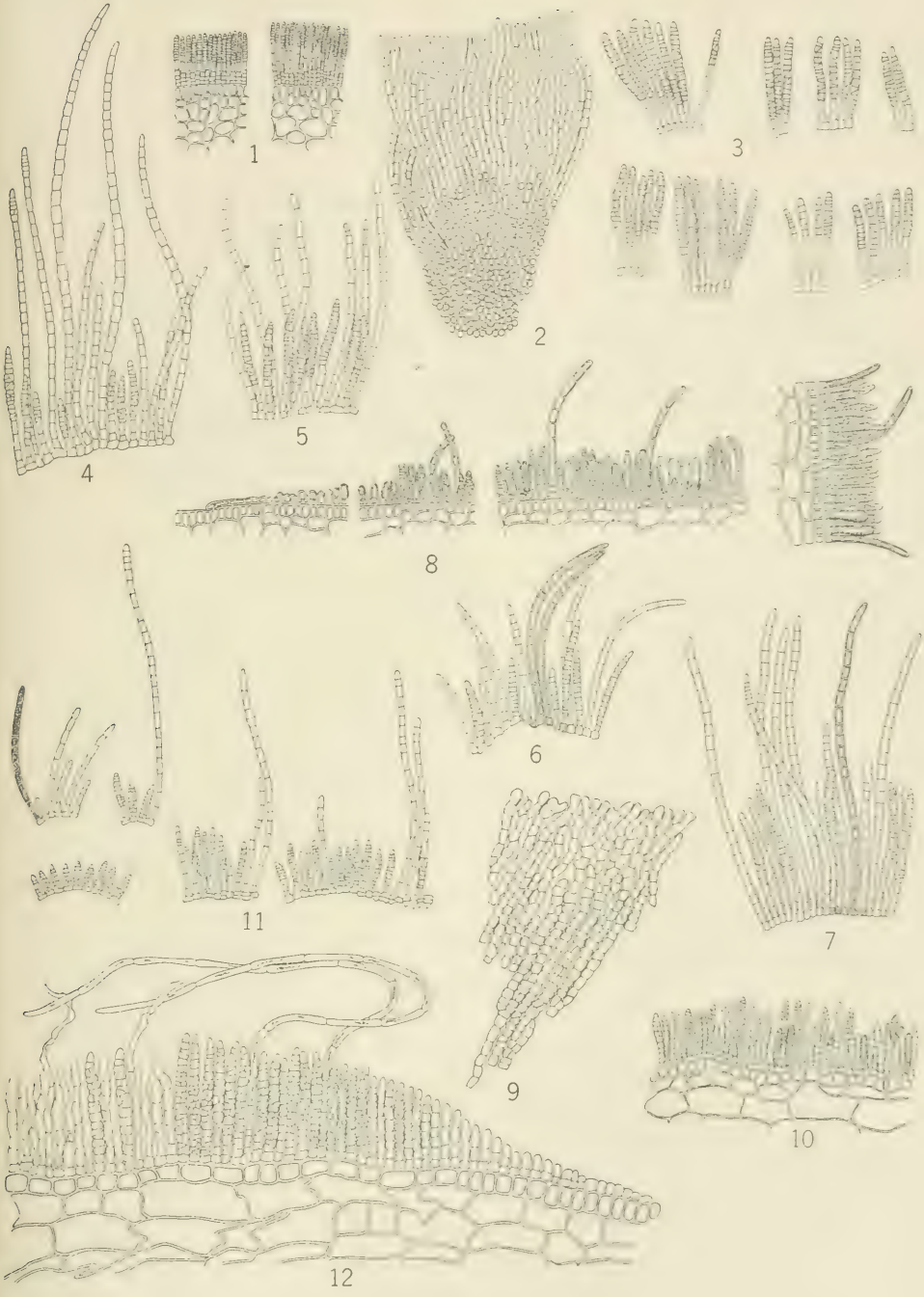
Fig. 10. A section of a characteristic frond showing the erect sterile filaments, gametangia, and "ascocysts." × 125.

Myrionema hecatonematoides S. and G.

Fig. 11. Five fragments showing the nature of the base, the shapes, sizes, and positions of the gametangia, and the erect filaments. × 125.

Myrionema primarium S. and G.

Fig. 12. A section through a typical frond and its host perpendicular to the latter. × 250.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III. NEW SPECIES OF COMPSONEMA

Introduction

The genus *Compsonema* was established by Kuckuck. We have accepted the genus to include forms which, like *Myrionema*, start from a single cell that, by divisions, soon originates a series of closely crowded, radiating filaments, forming a monostromatic basal layer more or less circular in outline; and which, unlike *Myrionema*, produce on erect filaments numerous gametangia that develop pluriseriate loculi. The genus is very closely related to the genus *Myrionema* on one side and to *Hecatonema* on the other. No species of this genus have previously been reported from the Pacific Coast of North America.

Compsonema streblonematoides sp. nov.

Plate 35, figure 4

Frondibus pulvinulos tenues, orbiculares, 3–5 mm. diam. formantibus; parte prostrata filamentis irregularitates hospitis arcte adhaerantibus composita, inferne ramulos radiciformes inter cellulas hospitis usque ad 300–350μ profunditate penetrantes, superne filamenta sterilia gametangiaque emittente; filamentis erectis 140–160μ longis; cellulis filamentorum erectorum cylindricis, 8.5–10μ diam., 1.5–3-plo longioribus; zoosporangiis ignotis; gametangiis plerumque cylindricis, brevi-pedicellatis, 55–70μ longis, 11–14μ latis; loculis plerumque 2-seriatis.

Growing on the pneumatocysts of *Nereocystis Luetkeana*. Mouth of Tomales Bay, Marin County, California. Type, Gardner, no. 3442*a* (Herb. Univ. Calif., no. 207035), August.

Compsonema streblonematoides, like a *Streblonema*, has a large part of the vegetative portion of the frond within the host-plant, the penetrating filaments extending into the host two to three times as far as the length of the external vegetative filaments. The whole frond, however, is the result of the growth of a single cell and forms a compact monostromatic basal disk. In the character of the gametangia it is close to a *Myrionema*, but in a very large majority of cases the loculi are biseriate.

Compsonema intricatum sp. nov.

Plate 35, figures 1–3

Frondibus 1.5–2.5 mm. altis, plus minusve confluentibus, stratum continuum velutinum indefinite expansum formantibus; filamentis repentibus numerosis, profuse ramosis, flectuantibus; filamentis erectis numerosis, aut simplicibus aut basim ramis paucis brevibus instructis, rectis, apice leviter attenuatis, pro parte piliferis; pilis veris deuntibus; cellulis filamentorum repentium forma magnitudineque irregularibus; cellulis filamentorum erectorum cylindricis, 8–9μ diam., 1–2-plo longioribus, ad basim filamentorum leviter angustioribus; chromatophoris taeniatis; zoosporangiis ovoideis usque ad ellipsoideis, in filamentis brevibus e filamentis repentibus oriundis terminalibus, in filamentis erectis prope basim pedicellatis sessilibusve, lateralibus, 25–33μ longis, 18–22μ latis; gametangiis in filamentis erectis brevibus e filamentis repentibus oriundis terminalibus, in filamentis erectis ad basim sessilibus pedicellatisve lateralibus, aut in filamentis primariis erectis intercalaribus, 80–120μ (usque ad 175μ) longis, 10–14μ latis, iis terminalibus intercalaribusque usque ad 600μ longis; loculis plerumque 2-seriatis.

Growing on *Fucus furcatus* f. Carmel Bay, Monterey County, California. Type, Gardner, no. 2893 (Herb. Univ. Calif., no. 207033), May.

Compsonema intricatum has diverged very far from a typical *Compsonema*. The size of a single individual at maturity cannot be ascertained, since the creeping filaments, and to some extent the erect filaments, are thoroughly and inextricably intertwined, forming continuous velvety strata on the surface of the host for several inches in expanse. The gametangia have, to a considerable degree, moved to the lateral position, the majority, however, remain terminal on long pedicels from the basal filaments. The lateral position is characteristic of *Ectocarpus*. The intercalary gametangia are typical of the genus *Pylaiella*. The creeping filaments are very numerous, although they do not radiate regularly side by side, thus forming a regular circular disk typical of the genus *Myrionema*. The zoosporangia(?) are numerous and develop with the gametangia on the same individual. It is exceedingly doubtful whether or not these structures are functional. At the stage in which the material was found, they were practically all of the same size, and some of the accompanying gametangia were empty. There is no indication of the formation of zoospores. They are filled with what seems to be densely crowded, angular chromatophores. The apical end is slightly beaked, and the outer wall dissolved, except a thin inner membrane. Their position on the same plants with gametangia, the peculiar open beak, and the

fact that they all seem to be of the same age lead us to suspect that they are some sort of abnormalities, or pathological conditions of the gametangia, which will require much more investigation to interpret. We are retaining this in the genus *Compsonema* on account of the prevailing simplicity of the erect filaments and the abundance of creeping filaments, practically every cell of which gives rise to an erect filament.

Compsonema fructuosum sp. nov.

Plate 36, figure 2

Frondibus pulvinulos orbiculares aut leviter irregulares, 4–5 mm. diam. formantibus; parte prostrata filamentis tortuosis repentibus irregularitates hospitis superficies arcte adhaerantibus; filamentis erectis simplicibus, dense stipatis, 190–230μ longis, cellulis cylindricis, 8–9μ diam., inferne 2–4-plo, superne 1–2-plo longioribus; chromatophoris taeniatis; pilis veris deuntibus; zoosporangiis sparsis, late clavatis, pedicellatis brevibus e filamentis repentibus oriundis suffultis, 55–65μ (usque ad 100μ) longis, 22–28μ latis; gametangiis in filamentis erectis terminalibus, cylindricis usque ad leviter fusiformibus, obtusis, 80–120μ longis, 12–16μ latis; loculis 2–4-seriatis.

Growing on the pneumatocysts of *Nereocystis Luetkeana*. Tomales Bay, Marin County, California. Type, Gardner, no. 3442 (Herb. Univ. Calif., no. 207034), August.

Compsonema fructuosum departs from the type of the genus *C. gracile* Kuckuck (1899, p. 90, pl. VI (12), figs. 6–9) in having a different host, in having no hairs, in having fewer and shorter sterile filaments, in having more gametangia and in having differences in details of measurements. In the abundance and position of the fruit and in the definite circular thallus with compact monostromatic basal layer of filaments, it approaches very closely to a typical *Myrionema*, but the multiseriate gametangia represent a stage in development which we have not admitted into that genus. The gametangia occupy a definite zone on the outer ends of the erect filaments. Practically all of the erect filaments bear gametangia.

At times the basal layer seems to be distromatic, or even polystromatic, but careful investigation shows that this appearance is occasioned by the overlapping creeping filaments which follow the very irregular surface of the host, due to the death of its surface layer of cells, probably before the epiphyte took possession. The zoosporangia are very sparse, but specimens have been seen which show undoubted zoospores.

Compsonema pusillum sp. nov.

Plate 37, figure 3

Frondibus pulvinulos tenues dilute fuscos, linea exteriore irregulares, 3–4 mm. diam. formantibus; parte prostrata filamentis tortuosis, ramosis, irregularitates superficies hospitis arcte adhaerante e latere infero filamenta pauca, brevia, et inter cellulas hospitis penetrantia emittente; filamentis erectis simplicibus, cylindricis, 270–300μ longis; cellulis filamentorum repentium maxime forma magnitudineque irregularibus; cellulis filamentorum erectorum cylindricis, 6–7μ diam., 3–5-plo longioribus; chromatophoris leviter interrupto-taeniatis; zoosporangiis sphaericis usque ad ovoideis, sessilibus aut pedicellis brevibus e filamentis repentibus oriundis suffultis, 18–25μ (usque ad 40μ) longis, 16–22μ latis; gametangiis cylindrico-conicis usque ad obtuse-fusiformibus, sessilibus aut pedicellis brevibus e filamentis repentibus oriundis suffultis, 40–60μ longis, 10–12μ latis; loculis 1–2-seriatis.

Growing on the pneumatocysts of *Nereocystis Luetkeana*. Carmel Bay, Monterey County, California. Type, Gardner, no. 3582 (Herb. Univ. Calif., no. 207036), January.

Compsonema pusillum seems to overlap each of several genera. Its zoosporangia, gametangia, and penetrating filaments ally it with *Streblonema*. Sauvageau (1897) has figured *Myrionema* with rhizoids. The gametangia are very small and have about as many uniseriate as biseriate loculi. It might be considered a very minute creeping *Ectocarpus*. We have placed it in the genus *Compsonema* on account of the scarcity of fruit in proportion to the sterile tissue, and on account of the monostromatic base, believing that the penetrating filaments are more or less accidental on account of the injured condition of the surface layer of cells of the host.

Compsonema speciosum f. **piliferum** f. nov.

Plate 38, figures 1, 2

Frondibus pulvinulos linea exteriore plus minusve orbiculares, 5–8 mm. diam. formantibus; filamentis repentibus maxime irregulariter et profuse ramosis, irregularitates superficies hospitis arcte alhaerantibus, interdum ramis brevibus inter cellulas incolumes hospitis penetrantibus; filamentis erectis numerosis, simplicibus aut ramos breves secundos, fructiferos aut interdum ramum piliferum emittentibus, 500–800μ longis, basim attenuatis, superne piliferis; cellulis filamentorum repentium forma magnitudineque maxime irregularibus; cellulis filamentorum erectorum cylindricis, basim 6–7.5μ diam., in parte latissima 9–12μ diam., usque ad 15-plo longioribus; chromatophoris taeniatis, in cellula quaque paucis; zoosporangiis obovoideis, 55–65μ longis, 28–32μ latis, raris; gametangiis filamentis repentibus oriundis

sessilibus aut in pedicellis longioribus brevioribusve, in filamentis erectis secundis, sessilibus pedicellatisve, aut rariore intercalaribus, gametangiis terminalibus 60–100μ longis, 14–18μ latis, gametangiis secundis variabilibus, parvioribus.

Growing on the pneumatocysts of *Nereocystis Luetkeana*. Moclips, Washington. Type, Gardner, no. 3812 (Herb. Univ. Calif., no. 207037), May.

Compsonema speciosum f. *piliferum* seems undoubtedly to be very closely related to *Myrionema speciosum* Börgesen [1902, pp. 421–424, which is the *Hecatonema speciosum* (Börgesen) Cotton, 1912, p. 15 (122) and the *Hecatonema diffusum* Kylin (cf. Cotton, *loc. cit.*)], at least the two sets of plants agree very closely in general habit and structure as described by Börgesen. Judging alone from the description and figures the chief differences are that our plant has short penetrating rhizoids, many terminal and no lateral hairs, and larger gametangia. We are unable to say that the plant would produce rhizoids on an uninjured host. The surface cells of the host are destroyed under the epiphyte, and it is an open question whether the penetrating rhizoids are or are not the cause of their death. Börgesen does not give the dimensions of the whole plant, but he states that the plants form short dense mats on the conceptacles of *Himanthalia lorea*, which would indicate that they were quite small. Our plants form circular cushions or mats 5–8 mm. in diameter. Typical zoosporangia were found at the base of the erect filaments. The lateral secund gametangia standing nearly perpendicular to the filaments of which the cell at the base in the filament becomes a part, is a character not found in *Compsonema gracilis* Kuckuck.

Compsonema sporangiiferum sp. nov.

Plate 36, figures 3–8

Frondibus pulvinulos orbiculares, 1–4 mm. diam. formantibus; parte prostrata filamentis compactis, irregularibus, plus minusve contortis, irregularitates superficies hospitis arcte adhaerantibus, monostromatica aut pro parte distromatica composita; filamentis erectis 300–700μ longis, simplicibus aut superne ramis paucis, brevibus, plerumque secundis, fructiferis indutis; cellulis filamentorum erectorum basim 6–8μ diam., 2–3-plo longioribus, apice 11–13μ diam., 1–1.5-plo longioribus, cellulis multis in parte superiore filamentorum 1–2-plo longitudinaliter divisis; chromatophoris taeniatis, in cellula quaque paucis; zoosporangiis numerosissimis, forma magnitudineque maxime variabilibus, anguste ellipsoideis, clavatis, usque ad late ovoideis, 40–130μ longis, 20–35μ latis, sessilibus aut pedicellis brevibus

e filamentis repentibus oriundis suffultis, aut in filamentis erectis lateralibus terminalibusve; gametangiis raris, cylindricis, in filamentis repentibus sessilibus brevi-pedicellatisve aut raro in filamentis erectis terminalibus tuberculatisque, 80–130μ longis, 11–15μ latis.

Growing on the pneumatocyst of *Nereocystis Luetkeana*. Neah Bay, Washington. Type, Gardner, no. 3859 (Herb. Univ. Calif., no. 207038), May.

The unusual condition in *Compsonema* prevails in *C. sporangiiferum*. The gametangia seem to be of rare occurrence. Examination of specimens of different sizes from different parts of the host revealed the presence of a large number of zoosporangia in all stages of development, many being empty. The gametangia are prevailingly near the base, although occasionally a complex one appears terminal on an erect filament. A very common character is the division of the cells in the upper parts of the filaments into 2–4 parts by longitudinal walls, producing a slight clavate condition in such filaments. We do not know, at present, the morphological significance of this condition. The zoosporangia and the gametangia, so far as observed, develop on distinct individuals.

Compsonema sessile sp. nov.

Plate 39, figure 6

Frondibus pulvinulos inconspicuos usque ad 1.5 mm. diam., in linea exteriore orbiculares usque ad irregulares formantibus; filamentis repentibus contortis, dense compactis, hospitem arcte adhaerantibus, ramulis radiciformibus deuntibus; filamentis erectis sparsis 20–24μ altis; pilis veris deuntibus; cellulis filamentorum repentium forma magnitudineque irregularibus, 9–12μ diam.; chromatophoris taeniatis in cellula quaque singulis; zoosporangiis ignotis; gametangiis numerosis, in filamentis repentibus sessilibus, conicis usque ad fusiformibus, 16–22μ longis, 11–14μ latis, parietibus multorum loculorum obliquis.

Growing on the lamina of *Hedophyllum sessile* near the outer end. Neah Bay, Washington. Type, Gardner, no. 3866 (Herb. Univ. Calif., no. 207039), May.

Compsonema sessile represents the extreme of the genus in the direction of simplicity. There are no hair filaments, and it is doubtful if any of the erect filaments remain sterile. At times even the cells of the basal layer seem to become a part of the gametangia, at least more than one cell in the basal layer may be at the base of a single gametangia. There would seem to be only a single modification of a *Myrionema* of the simplest type to produce this species, viz., the change in the type of gametangium from uniseriate to pluriseriate. If

we hold to the principal distinction between *Compsonema* and *Myrionema*, it will be necessary to ally this species with the former. It was found growing in company with *Streblonema aecidioides* f. *pacificum* S. and G., which gave to the host a roughened appearance, otherwise it probably would not be noticeable without microscopic examination.

Compsonema tenue sp. nov.

Plate 37, figure 6

Frondibus microscopicis, stratum plus minusve continuum in hospite inter algas parvas alteras formantibus; filamentis repentibus numerosis, ramosis, irregularitates superfices hospitis arcte adhaerantibus; filamentis erectis sparsis, simplicibus, apice basimque leviter attenuatis, 80–100μ altis; pilis veris sparsis; cellulis filamentorum repentium forma magnitudineque irregularibus; cellulis filamentorum erectorum cylindricis, non constrictis, 7–8μ diam., 1.5–2.5-plo longioribus; cellulis filamentorum piliferorum cylindricis, 5.5–6.5μ diam., inferne exacte aut fere quadratis, superne 7–10-plo longioribus; zoosporangiis(?) clavatis, 24–28μ longis, 8–10μ latis, sparsis; gametangiis fusiformibus usque ad irregulariter conicis, in filamentis repentibus sessilibus, numerosis, 22–28μ longis, 7–11μ latis; loculis plerumque 2-seriatis.

Growing on the fruiting fronds of *Cystophyllum geminatum*. Sitka, Alaska. Type, Gardner, no. 3972 (Herb. Univ. Calif., no. 207040), July.

Compsonema tenue, though scarcely typical of the genus, seems to possess affinities as closely allied to *Compsonema* as to any other genus, and hence we are placing it here for the present.

Compsonema nummuloides sp. nov.

Plate 35, figures 5, 6

Frondibus pulvinulos tenues orbiculares, 7–12 mm. diam. formantibus; parte prostrata filamentis radiantibus, multo crispatis, dense compactis, irregularitates superficies hospitis arcte adhaerantibus composita; filamentis erectis simplicibus, numerosis, 300–400μ longis, apice basimque leviter attenuatis; pilis veris deuntibus; cellulis filamentorum repentium forma magnitudineque multo irregularibus; cellulis filamentorum erectorum cylindricis, basim 6–7μ diam., 3–8-plo longioribus, in parte latissima 9–11μ diam., cellula apicali quadrata 6–7μ diam., 3–8-plo longiore; zoosporangiis ignotis; gametangiis plerumque sessilibus aut brevi-pedicellatis, nunc in filamentis erectis terminalibus, 70–90μ (usque ad 140μ) longis, 11–15μ latis; loculis plerumque 2-seriatis.

Growing on the pneumatocysts of *Nereocystis Luetkeana*. Moss Beach, San Mateo County, California. Type, Gardner, no. 4318 (Herb. Univ. Calif., no. 207041), July.

Compsonema nummuloides forms thin, light brown cushions on the pneumatocysts of the host. The whole cushion is a single plant, circular in outline and attaining a diameter of twelve or more millimeters, although the majority of the plants are much smaller. Like a typical *Myrionema* the plant starts from a single cell and by divisions forms a series of filaments radiating in all directions with apical growth and dichotomous branching, by the splitting of the apical cell, thus forming a continuous monostromatic layer of cells. Beginning in the center, practically every cell in each radiating filament of the basal layer gives rise successively to an erect filament, about two-thirds of which are fructiferous, the others remaining sterile. A very large majority of the gametangia are sessile or on short pedicels, thus occupying a zone near the creeping filaments, a *Myrionematoid* character, but the remainder of the filaments continue to grow and attain a length of 300–400μ. Some of these filaments are terminated by relatively short gametangia. This is one of several species with this general method of development which has been found growing only on the above mentioned host, differing from each other and from the type of the genus, *C. gracile* Kuckuck, in the size of the plant as a whole, in details of dimensions of their parts, in the presence or absence of zoosporangia and hairs, in the position of the gametangia, and in the relative amount of sterile filaments. It seems to form a fairly compact group but with overlappings, however, in the genera *Streblonema, Myrionema,* and *Hecatonema.*

Compsonema fasciculatum sp. nov.

Plate 38, figures 7–9

Frondibus floccules microscopicos plus minusve confluentes formantibus; filamentis repentibus tortuosis, hospitem sine ramulis radiciformibus adhaerantibus; filamentis erectis prope basim ramosis, 90–130μ longis, basim apiceque attenuatis, non piliferis, ad dissepimenta constrictis; pilis veris deuntibus; cellulis filamentorum erectorum in parte latissima, 10–14μ diam., 1–2-plo longioribus; zoosporangiis ignotis; gametangiis forma moderate irregularibus, conicis usque ad fusiformibus, 35–45μ longis, 12–18μ latis; plerumque lateralibus, brevipedicellatis.

Growing on *Gigartina radula* f. Pacific Grove, California. Type, Gardner, no. 4503 (Herb. Univ. Calif., no. 207042), December.

This species is allied here rather than with *Ectocarpus* because of its extremely small size and its creeping, fasciculate habit.

Compsonema myrionematoides sp. nov.

Plate 36, figure 1

Frondibus pulvinulos parvos, orbiculares usque ad irregulares, 1–2.5 mm. diam. formantibus; parte prostrata arcte monostromatica, filamentis dense compactis, tortuosis, radiantibis composita; filamentis erectis simplicibus, cylindricis, 110–130μ longis; pilis veris deuntibus; cellulis filamentorum repentium forma cylindricis usque ad irregularibus; cellulis erectorum cylindricis, 7.5–8.5μ diam., 1–2-plo longioribus, terminalibis plerumque plurimo longioribus; chromatophoris leviter interrupto-taeniatis, in quaque cellula singulis; zoosporangiis(?) late clavatis sessilibus aut brevi-pedicellatis e cellulis filamentorum repentium oriundis, 35–50μ longis, 20–28μ latis; gametangiis numerosis, cylindricis usque ad fusiformibus sessilibus aut brevi-pedicellatis e cellulis filamentorum repentium orundis, 50–70μ (usque ad 100μ) longis, 9–12μ latis.

Growing on the stipe of *Nereocystis Luetkeana*. Pacific Grove, California. Type, Gardner, no. 4510 (Herb. Univ. Calif., no. 207043), December.

There is but little choice as to the generic position of this small alga. It forms small brown tufts or cushions of loose filaments. Very frequently the gametangia are wider in the middle than at the ends and have decidedly biseriate loculi. Because of the more or less loose tufted character of the erect filaments and the partially biseriate gametangia we are placing it with the genus *Compsonema*.

Compsonema secundum sp. nov.

Plate 37, figures 1, 2

Frondibus parvissinus, plerumque plus minusve confluentibus; parte prostrata monostromatica, filamentis crispatissimis, ramosis composita; cellulis filamentorum repentium forma irregularibus, 7–8μ diam., longitudine variabilibus; filamentis erectis usque ad 1.25 mm. altis, simplicibus aut raro ramulis paucis brevibus fructiferis instructis; cellulis filamentorum erectorum cylindricis, basim 5.5–6.5μ diam., 4.5–6-plo. longioribus, in parte latissima 9.5–10.5μ diam., cellulis terminalibus usque ad 9-plo longioribus quam latis; chromatophoris taeniatis; zoosporangiis late clavatis, 60–90μ longis, 22–28μ latis, sessilibus aut brevi-pedicellatis e cellulis filamentorum repentium oriundis; gametangiis maxime variabilibus, raro pedicellis brevibus e filamentis repentibus oriundis suffultis, interdum per transformatione partis superioris filamenti erecti longi extensis, nunc simplicibus, nunc prolificationes numerosas laterales, breves plerumque secundas, raro oppositas producentibus, usque ad 400μ longis, 11–15μ latis, obtusis, clavatis.

Growing on the pneumatocyst of *Nereocystis Luetkeana*. West coast of Washington (Moclips) to central California (Carmel Bay). Type, Gardner, no. 4547 (Herb. Univ. Calif., no. 207044), Carmel Bay, California, December.

Like *Compsonema ramulosum*, *C. secundum* has gametangia occupying a variety of positions and assuming a diversity of forms. The form of gametangium which marks the species is the long terminal form which develops numerous, short, blunt-conical, seriate, secund, sessile gametangia, thus forming a complex composed of these gametangia and the metamorphosed cells in the upper part of the filament. The end of the filament becomes reflexed, at times almost scorpioid. The specimen from Moclips, Washington, was taken in May and the gametangia were practically all empty. The other parts of the plants manifested signs of old age conditions. They seem to belong to this species, but the filaments have a considerably greater diameter. Typical zoosporangia with well formed zoospores have been observed in this collection.

Compsonema ramulosum sp. nov.

Plate 39, figures 1–5

Frondibus pulvinulus orbiculares, 5–7 mm. diam. formantibus; parte prostrata monostromatica, filamentis plus minusve contortis et irregulariter ramosis, radiantibus composita; filamentis erectis pro parte piliferis simplicibus aut ramos breves plerumque fructiferos, secundos et interdum pilos ferentibus, basim leviter attenuatis; cellulis filamentorum repentium 6–7μ diam., quadratis aut leviter longioribus quam latis; cellulis filamentorum erectorum basim 6–7.5μ diam., superne leviter latioribus, 1–3.5-plo longioribus; cellulis ramorum pilorumque 4–6μ diam.; chromatophoris taeniatis, plus minusve interruptis angularibusque; zoosporangiis(?) late clavatis, terminalibus pedicellis longioribus bervioribusve suffultis aut prope apices filamentorum erectorum lateralibus, secundis aut verticillatis; gametangiis forma, magnitudine et positione maxime variabilibus, in filamentis repentibus sessilibus pedicellatisve, in filamentis erectis lateralibus, aut in filamentis primariis aut in ramulis lateralibus brevibus intercalaribus terminalibusve, clavatis, cylindricis, usque ad cylindrico-conicis, usque ad 140μ longis, 16μ latis; loculis plerumque 2-seriatis.

Growing on the pneumatocysts of *Nereocystis Luetkeana*. Carmel Bay, Monterey County, California. Type, Gardner, no. 4549 (Herb. Univ. Calif., no. 207045), December.

There exists in this species extreme variation in the form, size, and position of the gametangia. Some are sessile on the creeping filaments, though they are more frequently to be found on the pedicels up to

fifteen cells long. At times sessile forms are to be found on the erect filaments about two-thirds of the way up to the apex, but more generally they are terminal on small lateral ramuli on the erect filaments arising from the middle to near the apices. Rarely there are small lateral forms on the ramuli. Finally, they may rarely be terminal or intercalary and seriate on the erect filaments although the erect filaments are usually piliferous. The terminal forms on pedicels, and particularly on the main erect filaments, are often quite blunt, even clavate. Others on the prostrate filaments are narrow and sharply attenuated, at times terminated by a sterile pointed filament, in effect intercalary. Many of the gametangia, terminal on the ramuli, are composed of a single series of loculi. Most of the others are two or more seriate. The hair filaments do not seem to be abundant. They arise laterally on the main filaments, usually above the center. The meristem in these hairs is at the base which is surrounded by a sheath similar to that described by Sauvageau (1897, p. 47) for *Myrionema*. The ramuli are decidedly curved upwards.

The species is similar to *Myrionema speciosum* from the Faeröes, described by Börgesen (1902, p. 421). Our plant is more slender in all of its parts, has much longer gametangia, and possesses, in addition to the sessile, secund gametangia figured by Börgesen, occasional intercalary ones and many terminal ones on the numerous clustered ramuli. These ramuli are in turn occasionally branched, usually arise in groups, sometimes whorled, two or three arising from the same cell, in other instances they are secund.

The species often grows in association with other members of the Myrionemataceae and the Ectocarpaceae. As a rule, the main erect filaments do not enter into the formation of gametangia, but give rise either to sessile gametangia or to the ramuli. No zoospores have been observed in the so-called zoosporangia. We suspect that these may represent pathological conditions.

Compsonema serpens sp. nov.

Plate 39, figure 7

Frondibus stratum plus minusve expansum in superficie hospitis formantibus; parte repente filamentis multo contortis, irregulariter ramosis composita; filamentis erectis simplicibus aut raro superne ramis paucis subulatis indutis, inferne leviter attenuatis, superne gradatim attenuatis, non piliferis, 375–425μ longis; pilis veris deuntibus; cellulis filamentorum repentium cylindricis ad dissepimenta usque ad irregularibus, 10–13μ diam., 0.5–3-plo pongioribus; cellulis

filamentorum erectorum cylindricis non constrictis, basi 5.5–8.5μ diam., in parte latiore, 10–17μ diam., 1.25–2.5-plo longioribus; chromatophoris taeniatis, in cellulis juvenis dense aggregatis, in cellulis senioribus numerosissimis et segregatis; zoosporangiis ignotis; gametangiis cylindrico-conicis, in pedicellis longioribus brevioribusve e filamentis repentibus oriundis terminalibus, raro in filamentis longis erectis terminalibus, 60–130μ longis, 18–28μ latis.

Growing on the sterile base of *Gigartina radula* f., in company with several other small algae. Cypress Point, Monterey County, California. Type, Gardner, no. 4684 (Herb. Univ. Calif., no. 207046), December.

This diminutive member of the Melanophyceae is on the border line between *Compsonema* and *Ectocarpus*. Our comprehension of these two genera, so far as the vegetative portion is concerned, is that a typical *Compsonema*, starting from a single cell, develops an extensive, creeping, attaching mass of filaments, radiating in all directions from the origin, which later produces very numerous erect filaments, some of which may remain sterile and others become fructiferous; and that a typical *Ectocarpus*, starting likewise from a single cell, develops a rather insignificant series of attaching filaments, more or less rhizoidal in nature, and a relatively extensive system of erect filaments finally producing the fruit. Starting with this conception concerning the two genera, we are assuming that differentiation has proceeded from *Compsonema* in the direction of the reduction of the creeping portion, to a more extensive development of the erect portion, finally resulting in an *Ectocarpus*.

The species under consideration has a relatively extensive system of creeping filaments but very much less so than that of a typical *Compsonema*. The creeping filaments do not form a solid disk, but those from different plants are so intertwined that it is impossible to determine the limits of a distinct individual. In this character it resembles an *Ectocarpus*. The gametangia are like those of a typical *Ectocarpus*, but since they are mostly short pedicellate and spring directly from the creeping filaments, as is the case in a typical *Compsonema*, and because of the relatively extensive system of creeping filaments, we have placed it in the latter genus.

Compsonema coniferum sp. nov.

Plate 38, figure 3

Frondibus microscopicis, plus minusve confluentibus, stratum velutinum in superficie hospitis algis alteris minutis immixtis formantibus; parte prostrata filamentis profuse ramosis, multo contortis composita; filamentis erectis numerosis, simplicibus, apice basimque leviter attenuatis, non piliferis, 150–200μ altis; pilis veris deuntibus; cellulis filamentorum repentium forma magnitudineque irregularibus, 6–7.5μ latis, 9–12μ longis; cellulis filamentorum erectorum cylindricis usque ad leviter doliiformibus in parte latiore, 8–10μ diam., 1–1.5-plo longioribus; chromatophoris taeniatis; zoosporangiis ignotis; gametangiis sessilibus aut in pedicellis brevibus e filamentis repentibus oriundis, angusta conicis, 46–65μ longis, 15–18μ latis.

Growing on the sterile base of *Gigartina radula* f. Cypress Point, Monterey County, California. Type, Gardner, no. 4684*a* (Herb. Univ. Calif., no. 207047), December.

Compsonema coniferum seems to be a very close relative of *C. fasciculatum*, found growing on the same host. The fronds are more extensive, unbranched, and have larger gametangia. We consider this species of *Compsonema* a very near approach to an *Ectocarpus* of extremely small size. We are inclined toward the genus *Compsonema* as a more appropriate genus for this species than *Ectocarpus* on account of its extensive creeping habit and prolific production from the creeping filaments of nearly sessile gametangia and many sterile erect filaments. It is to be found quite commonly associated on the same host with several other species of Myrionemataceae.

Compsonema dubium sp. nov.

Plate 38, figure 6

Frondibus diminutivibus, floccules parvos inter algas microscopicas alteras in hospite formantibus; parte prostrata filamentis multo contortis, ramosis, repentibus composita; filamentis erectis simplicibus, totaliter prope exacte cylindricis, 275–350μ longis, non piliferis; pilis veris deuntibus; cellulis filamentorum repentium forma magnitudineque maxime variabilibus; cellulis filamentorum erectorum cylindricis, medio 7–9μ diam., superne inferneque minoribus, 2–3-plo longioribus; zoosporangiis(?) ellipsoideis, terminalibus, brevi-pedicellatis 16–22μ longis, 12–15μ latis; gametangiis cylindricis usque ad leviter fusiformibus, in pedicellis longioribus brevioribusve filamentis repentibus oriundis, terminalibus, raro in filamentis longis erectis terminalibus, 50–75μ longis, 8–11μ latis; loculis plerumque 2-seriatis.

Growing on the sterile base of *Gigartina radula* f. Cypress Point, Monterey County, California. Type, Gardner, no. 4684*d* (Herb. Univ. Calif., no. 207048), December.

Compsonema dubium, like *C. coniferum* and *C. serpens*, has close affinities with small members of the genus *Ectocarpus*. Its relatively long and narrow gametangia distinguish it from the two species here mentioned, with which it is frequently associated.

Compsonema secundum f. terminale f. nov.

Plate 37, figures 4, 5

Frondibus stratum indefinite expansum, velutinum, per filamenta maxime distorta, ramosa, repentia, per ramulos radiciformes, numerosis, penetrantes, e superficie infera oriendes affixum formantibus; filamentis erectis 700–800μ (usque ad 1 mm.) longis, simplicibus aut ramulos paucos, breves, secundos, fructiferos producentibus, rectis, basim leviter attenuatis, superne cylindricis; cellulis filamentorum repentium et ramulorum radiciformium irregularibus, magnitudine variabilibus; cellulis filamentorum erectorum cylindricis, ad dissepimenta non constrictis a 6–8μ diam., basi 2–3.5-plo, superne 0.5–2-plo, longioribus; chromatophoris irregulariter taeniatis, in cellula quaque paucis; zoosporangiis(?) late clavatis, e filamentis repentibus oriundis, 50–60μ longis, 18–22μ latis, sessilibus, brevi-pedicellatisve, aut terminalibus seriatisque, proliferationibus lateralibus secundisque indutis; gametangiis e filamentis repentibus oriundis, sessilibus aut longepedicellatis, 90–110μ longis, 15–18μ latis, proxime cylindricis aut in filamentis erectis terminalibus, clavatis, frequenter prolongationibus tuberculatis, secundis et magnitudine variabilibus.

Growing on the pneumatocysts of *Nereocystis Luetkeana*. Central California (San Francisco and Pacific Grove). Type, Gardner, no. 4690 (Herb. Univ. Calif., no. 207049), Pacific Grove, December.

This form of *Compsonema* is to be distinguished by the great predominance of relatively short terminal gametangia, and many relatively large, lateral, secund, sessile gametangia which are curved upwards. There are a few sessile or short pedicellate examples at the base and a few lateral forms on short ramuli. Specimens taken in December had the larger number of gametangia empty.

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PLATE 35

Compsonema intricatum S. and G.

Fig. 1. A diagrammatic illustration of a part of a plant.

Fig. 2. A part of a plant showing a variety of forms of gametangia, lateral and pedicellate or sessile, terminal, and intercalary; also numerous zoosporangia(?) on the same plant and also, in some cases, on the same filament. × 125.

Fig. 3. A small part of a plant showing the acute erect filaments, and pedicellate gametangia and zoosporangia. × 225.

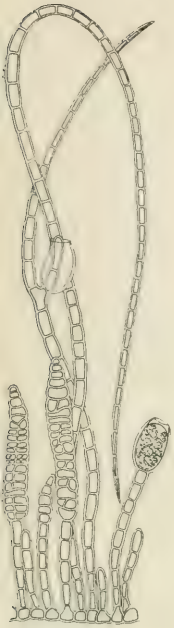
Compsonema streblonematoides S. and G.

Fig. 4. A part of a section through a plant and its underlying host, showing a basal filament on the surface and rhizoidal filaments penetrating into the host, and erect filaments and gametangia above. × 250.

Compsonema nummuloides S. and G.

Fig. 5. A segment of the sterile creeping filaments showing the method of branching. × 125.

Fig. 6. Eight fragments of plants showing the various shapes and positions of the gametangia and the character of the erect filaments. × 125



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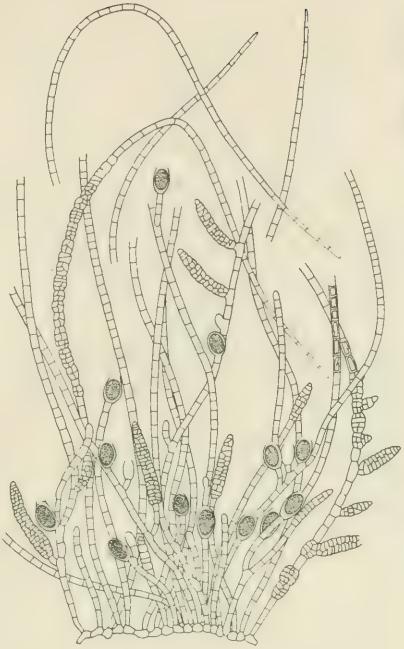

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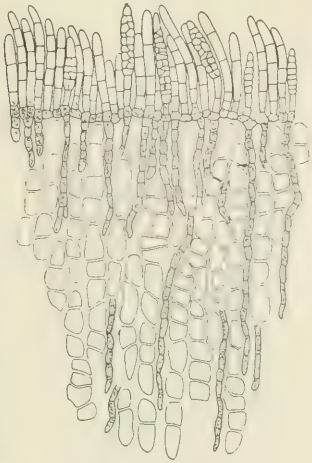

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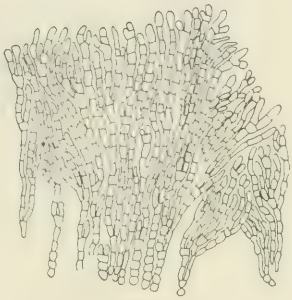

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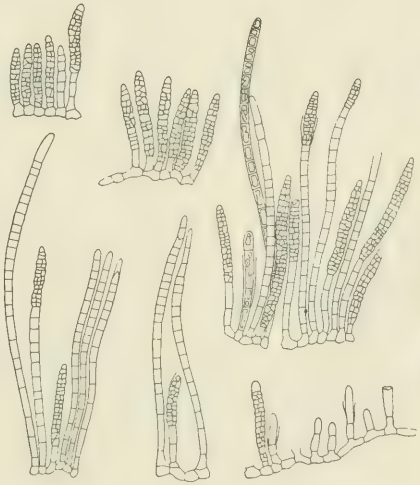

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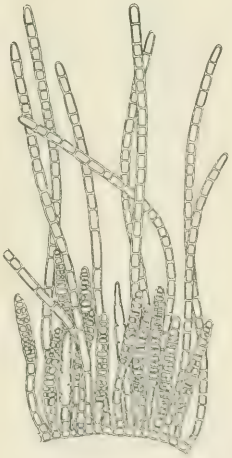

PLATE 36

Compsonema myrionematoides S. and G.

Fig. 1. Six fragments of plants showing the character and position of the gametangia, the basal filaments and the erect sterile filaments. × 125.

Compsonema fructuosum S. and G.

Fig. 2. A small part of a frond showing some abnormal developments of gametangia. Two are terminal on lateral branches. Two have developed in one old gametangium. One is terminal on a long pedicel growing up through an empty gametangium. × 250.

Compsonema sporangiiferum S. and G.

Fig. 3. A few fragments of erect filaments showing unusual terminal gametangia and terminal zoosporangia. × 125.

Fig. 4. A group of young gametangia and erect filaments. × 125.

Fig. 5. A fragment of a plant showing zoosporangia in various positions, some sessile on the basal filaments, some sessile and lateral and some terminal on the erect filaments. × 125.

Figs. 6, 7. Fragments of filaments showing lateral secund branching near the apices. × 125.

Fig. 8. Fragments showing positions of well developed zoosporangia. × 125.

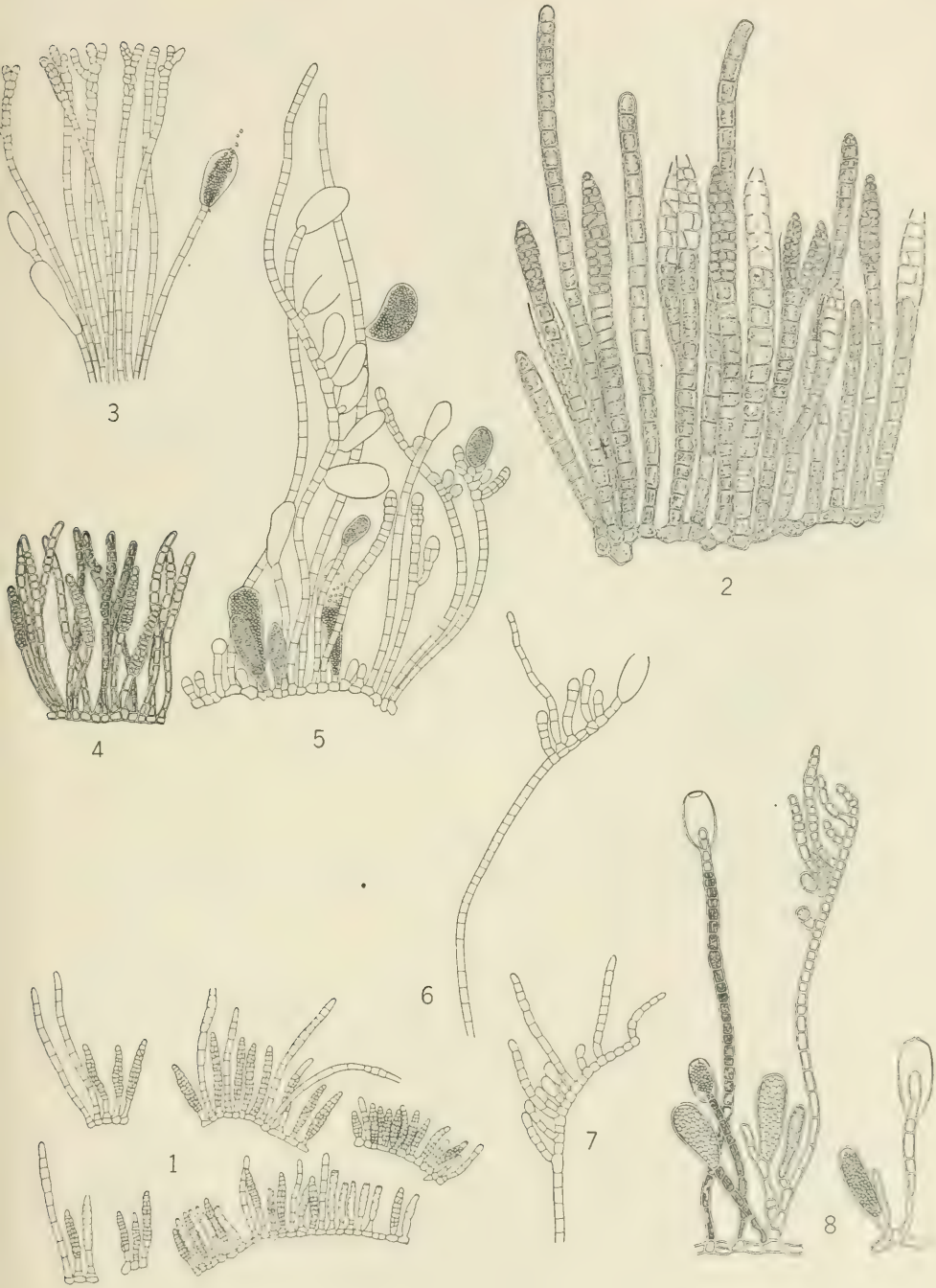
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PLATE 37

Compsonema secundum S. and G.

Fig. 1. Three fragments of plants showing small gametangia on short pedicels from a basal filament and complex terminal gametangia with mostly secund lateral developments. × 125.

Fig. 2. A fragment of a plant showing a modification in which the gametangia are mostly terminal and erect, and only rarely possessing lateral protuberances. × 125.

Compsonema pusillum S. and G.

Fig. 3. Three fragments of plants showing shapes and positions of zoosporangia and gametangia. Character of the creeping and of the erect filaments and a few branches pushing between the surface cells of the host. × 125.

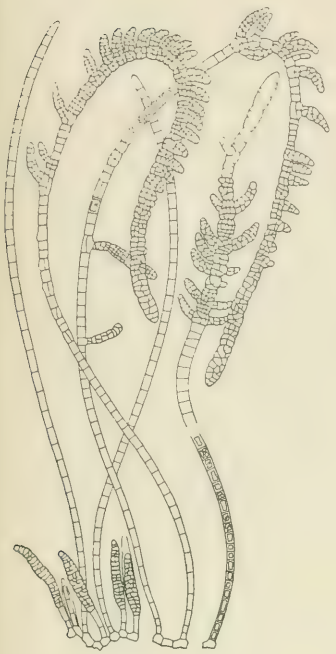
Compsonema secundum f. *terminale* S. and G.

Fig. 4. A fragment of a plant showing the characteristic terminal and large lateral gametangia. × 125.

Fig. 5. A filament which seems to be producing zoosporangia below an empty gametangium. × 125.

Compsonema tenue S. and G.

Fig. 6. Fragments of plants showing erect filaments, true hairs and zoosporangia (?) and gametangia sessile on the creeping filaments. × 250.



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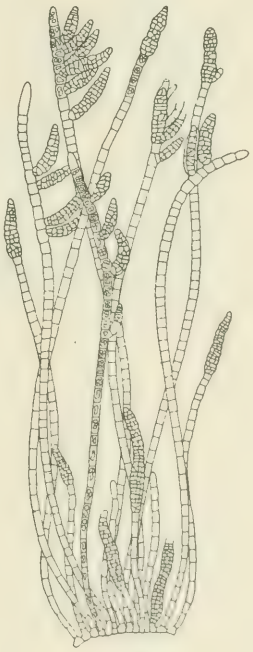

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PLATE 38

Compsonema speciosum f. *piliferum* S. and G.

Fig. 1. A fragment of a plant showing well developed rhizoids from the creeping filament, various shapes and positions of the gametangia and terminal hairs. × 125.

Fig. 2. A fragment showing a well developed zoosporangium with included zoospores. × 125.

Compsonema coniferum S. and G.

Fig. 3. Fragments of a frond, showing the characteristic shapes, sizes, and positions of the gametangia, and the character of the erect filaments. × 125.

Compsonema fructuosum S. and G.

Fig. 4. A fragment of a frond showing the character of the erect filaments and a well developed zoosporangium. × 125.

Fig. 5. A group of characteristic gametangia. × 125.

Compsonema dubium S. and G.

Fig. 6. Fragments of typical plants bearing gametangia. × 250.

Compsonema fasciculatum S. and G.

Figs. 7–9. Fragments of plants showing the positions, shapes, and sizes of the gametangia, the branching erect filaments and the tortuous character of the creeping filaments. × 250.

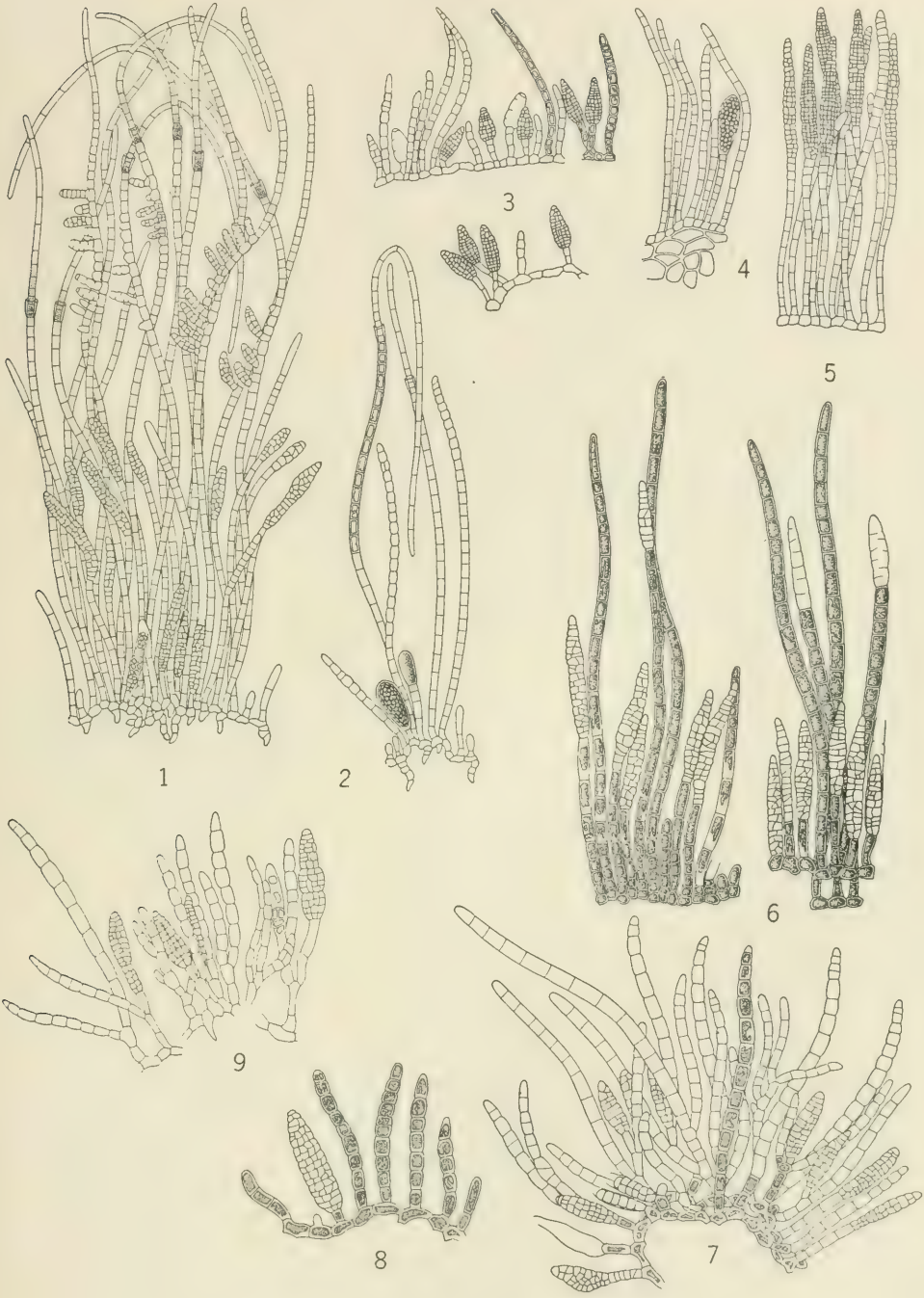
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PLATE 39

Compsonema ramulosum S. and G.

Figs. 1, 3, 4, 5. Fragments of plants showing the character of the creeping filaments, the abundance of erect filaments, the method of their branching, and the great variety in shapes, sizes, and position of gametangia. × 125.

Fig. 2. A fragment showing zoosporangia(?). × 125.

Compsonema sessile S. and G.

Fig. 6. A fragment of a typical plant sitting upon its host. × 250.

Compsonema serpens S. and G.

Fig. 7. Two fragments of typical plants. × 125.

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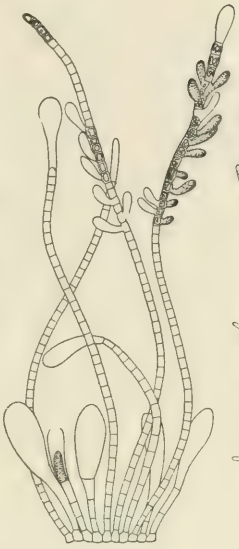

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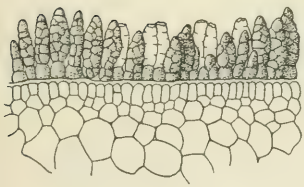

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IV. NEW SPECIES OF HECATONEMA

Introduction

The genus *Hecatonema* was established by Sauvageau (1897, p. 249). We have in the Herbarium of the University of California numerous collections of small epiphytic plants found upon *Nereocystis Luetkeana* in various localities on the Pacific Coast, which we have placed in the genus *Hecatonema*. This genus, as we interpret it, is quite similar to *Compsonema* and to *Myrionema*, but differs from each in having a distromatic base. Of the two, it seems more nearly akin to *Compsonema* than to *Myrionema* in that it develops gametangia with pluriseriate loculi instead of uniseriate, as is the case in *Myrionema*.

There have been no species of this genus reported previously on the Pacific Coast of North America. This study is but a preliminary one and it is hoped that it may stimulate further investigation of this genus as well as of the other closely related genera.

Hecatonema variabile sp. nov.

Plate 41, figures 1–12

Frondibus pulvinulos orbiculares, 4–7 mm. diam. formantibus; parte prostrata filamentis radiantibus subapicaliter ramosis, per ramulos radiciformes numeros, breves, 1–3-cellulates adhaerantibus composita; filamentis erectis non dense stipatis, non e centro ad peripheriam seriater evolvatis, simplicibus, 400–500μ longis; pilis veris ignotis; cellulis filamentorum repentium forma irregularibus, 7–9μ diam., margine 1–3-plo longioribus; cellulis filamentorum erectorum basim 4.5–5μ diam., 2–5-plo longioribus, apice 8–10μ diam., 1–3-plo longioribus; zoosporangiis(?) late clavatis in filamentis prostratis sessilibus brevi-pedicellatisve raro in filamentis erectis terminalibus lateralibusve, 50–65μ longis, 20–24μ latis; gamentangiis cylindricis, apice leviter attenuatis, in filamentis sessilibus brevi-pedicellatisve, raro in filamentis erectis terminalibus, 70–120μ longis, 9–12μ latis; loculi 1–2-seriatis.

Growing on the pneumatocysts of *Nereocystis Luetkeana*. Carmel Bay, Monterey County, California. Type, Gardner, no. 3109 (Herb. Univ. Calif., no. 207050), December.

From the standpoint of the structure of the gametangia, the type of this species of *Hecatonema* could scarcely be separated from a

Myrionema such as *M. phyllophylum* S. and G. They, in part, possess uniseriate loculi, but have many perpendicular and slanting walls, making a partial biseriate condition. The basal layer, particularly in the center of the thallus, is distinctly distromatic, developing numerous peg-like rhizoids, which serve to anchor it more firmly to the host, and, for the most part at least, the branching of the filaments is subterminal, whereas that of a true *Myrionema* is terminal and brought about by the splitting of the apical cell.

The size of the plants as a whole varies considerably. The material of the type varies in this respect from 4 mm. to 7 mm. in diameter. In some collections of specimens which we have included under the species, the specimens are as small as 2 mm. in diameter, in others they are up to 10 mm. in diameter. The length of the erect filaments varies from 150μ to 500μ. Mature gametangia vary from 55μ to 120μ long. The relative number of gametangia terminal on the erect filaments, as well as their size and complexity, is exceedingly variable in different collections. Two or three cells only may metamorphose in some filaments, in others eight or ten. Occasionally small lateral outgrowths from these metamorphosed cells may occur. The number of erect filaments in proportion to the number of gametangia is a character which seems to be very unstable. In some collections they exceed the number of gametangia almost two to one, in others they do not occur more than in proportion of one to five. They are very irregular in origin along the radiating creeping filaments. Some near the margin of the frond may be nearing maturity before others near the frond have started (pl. 41, fig. 5).

Hecatonema clavatum sp. nov.

Plate 40, figures 1–4

Frondibus pulvinulos orbiculares, 2–3 mm. diam., margine lato filamentis erectis destituta formantibus; parte prostrata per ramulos radiciformes numerosos, breves, subulatosque adhaerente, et filamentis regulariter radiantibus, dense compactis composita; filamentis erectis plerumque clavatis simplicibus, 190–210μ longis; cellulis filamentorum repentium 5–6μ diam., 1.5–2-plo longioribus; cellulis filamentorum erectorum inferne cylindricis, 5.5–6.5μ diam., 2–2.5-plo longioribus, superne ad discepimenta leviter constrictis, 8–11μ diam., 1.5-plo longioribus; zoosporangiis(?) in filamentis repentibus, sessilibus subsessilibusve, clavatis, 60–80μ longis, 10–14μ latis; gametangiis cylindricis usque ad leviter fusiformibus, in filamentis repentibus sessilibus brevi-pedicellatisve, 55–85μ (usque ad 110μ) longis, 8–12μ latis; loculis plerumque 2-seriatis.

Growing on the pneumatocysts of *Nereocystis Luetkeana*. Mouth of Tomales Bay, Marin County, California. Type, Gardner, no. 3456 (Herb. Univ. Calif., no. 207051), May.

The structures designated zoosporangia(?) in the above diagnosis of this species were found interspersed among the gametangia. No indication of the formation of zoospores has been observed, which leads to the suspicion that they may be abortive gametangia. The terminal cells of the erect filaments are often longer than the cells below it, and in these filaments in which the cells are divided lengthwise, producing the clavate condition, the terminal cell degenerates in a similar manner as do the hairs in other species. The longitudinal division of cells in the upper parts of the filaments is undoubtedly connected with the formation of the short, lateral, often secund, gametangia characteristic of nearly related species in *Hecatonema* and in *Compsonema*, for in a few instances such gametangia were observed in old specimens in which the gametes had, to a large degree, escaped from the characteristic gametangia.

Hecatonema Lawsonii sp. nov.

Plate 40, figures 5–7

Frondibus pulvinulos microscopicos, 250–500μ diam., linea exteriore irregulares formantibus; parte prostrata filamentis maxime contortis, profuse ramosis, subterminaliter furcatis composita; filamentis erectis stratum compactum valliforme filamenta pilifera numerosa sparsa includens formantibus, 0.75–1.5 mm. longis; cellulis filamentorum repentium radianter tangentialiterque divisis, in centro thalli pseudoparenchyma formantibus, forma irregularibus, 4–5μ diam.; cellulis filamentorum piliferorum basi quadratis et vaginatis, superne usque ad 25-plo longioribus quam latis; zoosporangiis ignotis; gametangiis cylindricis usque ad leviter fusiformibus, 25–30μ longis, 5–6.5μ latis; loculis multis per parieties longitudinales et obliquos formatis.

Growing on the sporophylls of *Nereocystis Luetkeana*. Uyak Bay, Alaska. Type, Setchell and Lawson, no. 5131 (Herb. Univ. Calif., no. 99357), August.

Myrionema vulgare Collins, Holden and Setchell, Phyc. Bor.-Amer. (Exsicc.), no. 924 (non Thuret). *Myrionema strangulans* Setchell and Gardner, Alg. N. W. Amer., 1903, p. 249 (non Grev.).

This plant superficially resembles very closely *Myrionema foecundum* f. *simplicissimum* S. and G. Microscopic examination, however, reveals several important differences. The creeping filaments are unique. The branches are very numerous, come off at wide angles and seem, for the most part at least, to be subterminal, or if the terminal

cell splits, one of the dichotomy very frequently fails to develop till much later. Many of the cells in the center, and even toward the periphery, divide radially and perpendicular to the surface of the host, forming a pseudoparenchymatous layer. Thus this species, strictly speaking, cannot be said to be distromatic, since the distromatic condition of a frond is really brought about by *radial* divisions of the cells of filaments, but parallel to the surface of the host. The character of the gametangia and of the creeping filaments will not permit of its being placed with *Myrionema vulgare* Thuret as further described and figured by Sauvageau (1897, p. 186, *et seq.*). On account of the radial divisions of the creeping filaments and the prevailing biseriate condition of most of the gametangia, we are placing this species with the genus *Hecatonema* and dedicating it to Professor A. A. Lawson, one of the collectors.

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1897. Sur quelques Myrionémacées. Ann. sci. nat., 8 sér., Bot., vol. 5, pp. 161–288.

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1903. Algae of Northwestern America. Univ. Calif., Publ. Bot., vol. 1, pp. 165–418, pls. 17–27.

PLATE 40

Hecatonema clavatum S. and G.

Fig. 1. A section through a typical mature plant showing penetrating rhizoids from the basal layer, the clavate, sterile, erect filaments, and typical gametangia. × 250.

Fig. 2. The same as figure 1, but showing "ascocysts." × 250.

Fig. 3. A small fragment without rhizoids. × 125.

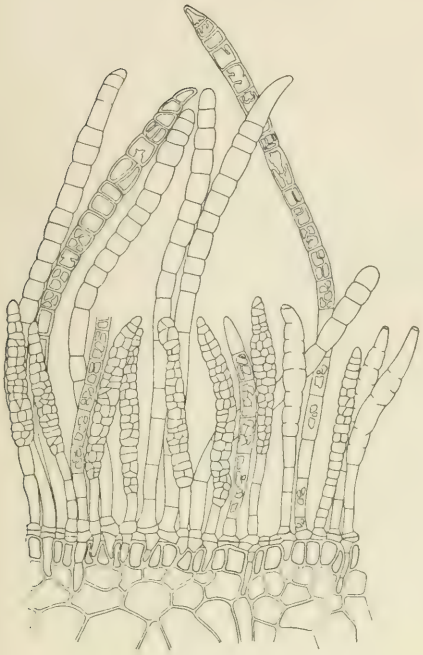
Fig. 4. A segment of the base at its margin. × 250.

Hecatonema Lawsonii S. and G.

Fig. 5. Two segments of the base showing frequent radial divisions of the cells. × 250.

Fig. 6. A young plant before any erect filaments have begun to develop. × 250.

Fig. 7. Typical gametangia and true hairs. × 250.



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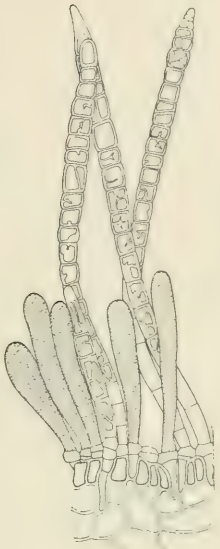

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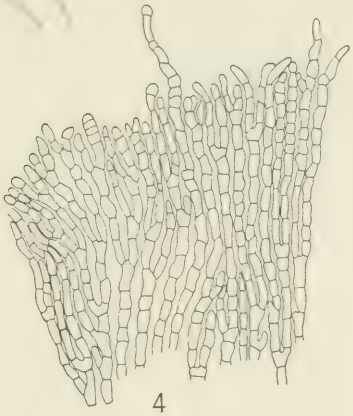

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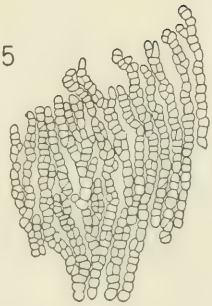

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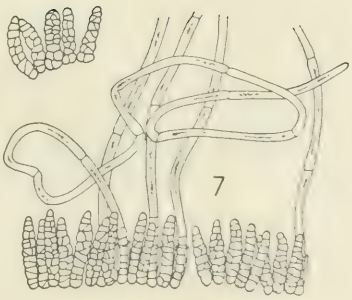

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PLATE 41

Hecatonema variabile S. and G.

Fig. 1. Five fragments of plants taken near the margin of the frond. × 125.

Fig. 2. Three fragments, older than figure 1, showing secondary growth within the empty gametangia. × 125.

Fig. 3. A group of sessile gametangia. × 125.

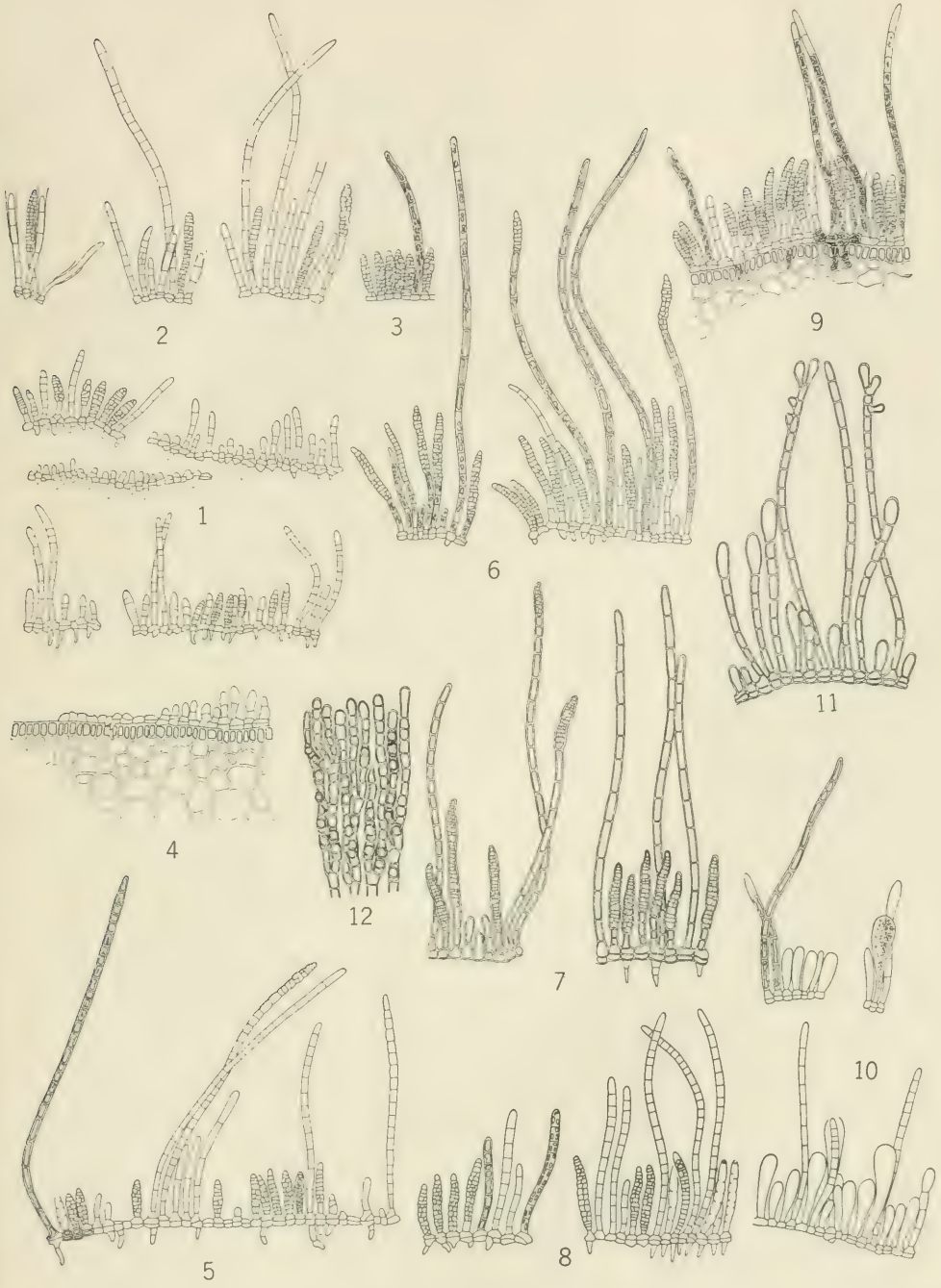
Fig. 4. Terminal part of a creeping filament seemingly showing the early stages in the development of the zoosporangia. × 125.

Fig. 5. A part of a creeping filament showing the heterogeneous development of erect filaments. × 125.

Figs. 6, 7, 8, 9. Typical fragments of mature fronds. × 125.

Figs. 10, 11. Fragments with zoosporangia. × 125.

Fig. 12. A segment of the base. × 125.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V. NEW SPECIES OF PYLAIELLA AND STREBLONEMA

Pylaiella tenella sp. nov.

Plate 42, figures 9–11

Frondibus late diffusis, simplicibus, 0.5–0.75 mm. altis, superne longe-attenuatis, non piliferis, per filamenta curta, ramosa, contortaque affixis; cellulis 7–10μ diam., 1–2.5-plo. longioribus quam latis; chromatophoris juvenis, singulis, interrupto-taeniatis, cellulam fere implentibus, ultimo in frustis distinctis separantibus; zoosporangiis longe-catenatis subterminalibus, cellulis numerosis assimilatoribus in seriebus per divisiones longitudinales zoosporangiis bina aut quaterna formantibus; gametangiis subterminalibus.

Growing on *Pleurophycus Gardneri* Setchell and Saunders, the plants forming minute tufts, which later become confluent. Neah Bay, near Cape Flattery, Washington. Type, Gardner, no. 3818 (Herb. Univ. Calif., no. 207010), May.

This species of *Pylaiella* is the most diminutive of all the known species of the genus, rarely attaining the length of one millimeter, its nearest rival, in this respect, being *P. nana* of Kjellman, from the Norwegian Polar Sea. It differs from that species in size, being only about one-half as large, in not being branched, in having subterminal gametangia in a long series, instead of terminal branched ones as described and figured by Kjellman for *P. nana* and in having double and quadruple zoosporangia formed by longitudinal and cross divisions of fructiferous cells. We have also observed this condition highly developed in forms of *P. littoralis*. Double zoosporangia have been observed by Börgesen (1920, p. 433) in *P. fulvescens* (Schousb.) Bornet from the Danish West Indies. It evidently belongs to the Panthocarpus group of the genus as established by Skottsberg (1915, p. 158). The gametangia are formed by the transformation of vegetative cells, usually beginning relatively few cells back of the apices of the filaments, a considerable number of cells transforming simultaneously. The transformation continues in both directions until one-half to three-fourths of the filament is converted into gametangia. They vary greatly in size, some producing as many as thirty-two loculi from a single assimilating cell. They may be continuous or discontinuous, certain assimilating cells in the series not being transformed. The cell walls in the formation of loculi frequently are quite oblique.

Zoosporangia occupy very much the same position in the filaments as the gametangia. They are subterminal, long-catenate, but seem to be formed more nearly simultaneously than are the gametangia.

These plants are quite abundant on the blade of the host-plant at Neah Bay. We have not observed it growing elsewhere, although the host is abundant in the vicinity of the Strait of Juan de Fuca. They are, however, very inconspicuous, forming small, more or less continuous expansions, barely recognizable when the host plant is wet.

Pylaiella unilateralis sp. nov.

Plate 42, figures 6–8

Filamentis erectis per filamenta repentia, irregularia, plus minusve ramosa affixis, floccosis, leviter clavatis, 4–7 mm. altis, basi 19–22μ diam., apicali 28–32μ diam., ramis inferne plerumque alternis sparsisque, superne secundis, e cellulis 1–2-plo longitudinaliter divisis oriendis; cellulis 2–2.5-plo longioribus quam latis, basi cylindricis, superne plus minusve quadratis doliiformibusque; chromatophoris tenuibus, irregulariter taeniatis et plus minusve connectis; zoosporangiis eodem tempore maturantibus, 7–12-catenatis, in ramulis plerumque terminalibus, sphaeroideis, 24–28μ diam.; gametangiis ignotis.

Growing on rocks in shallow pools, near high-tide limit. Sunset Beach, near the mouth of Coos Bay, Oregon. Type, Gardner, no. 2748 (Herb. Univ. Calif., no. 207011), May, 1914.

The secund branching, together with the longitudinal divisions of the cells from which the secund branches arise forming a polysiphonous region are the chief distinguishing characteristics of this species. The branching below is sparse, alternate or very rarely opposite, and the branches are relatively long and attenuated. These branches may give rise to terminal zoosporangia, or to a few short alternate ramuli which in turn produce the zoosporangia. Many of the main filaments become slightly enlarged toward their outer ends, the cells becoming nearly quadrate, their walls thickened, and their contents very dense. An average of about thirty-five cells, though frequently as many as sixty-five, are thus transformed. A few cells of the ends of the filaments are not transformed and soon disintegrate, thus producing a distinctly clavate filament. The region of transformation seems to be a new meristem of a peculiar nature. Many of the cells divide once or, less frequently, twice, by longitudinal planes as a rule, but occasionally the dividing planes are at right angles separating the cell into four parts. The unique feature resulting from these divisions is the lack of further growth of the cells. Usually one

of the cells resulting from longitudinal division gives rise to a branch, shorter or longer, but similar to branches arising in the regular manner. The branches are typically secund, but may rarely come from the opposite side of the filament. Many of the main filaments become much curved in this branching region.

Streblonema Porphyrae sp. nov.

Plate 44, figure 6

Frondibus plerumque endophyticis; filamentis prostratis maxime tortuosis, inter parietes cellularum hospitis penetrantibus, copiose ramosis; filamentis erectis ultra superficiem hospitis leviter protrudentibus, passim ramosis; filamentis piliferis ignotis; cellulis filamentorum repentium 3–4μ diam., forma irregularibus; zoosporangiis ignotis; gametangiis filamenta erecta terminantibus, ultra superficiem hospitis leviter protrudentibus, forma fusiformibus ad irregularibus, 25–35μ longis, 5–8μ latis.

Growing in the parenchymatous base of *Porphyra naiadum* on eelgrass. Pacific Grove, California. Type, Gardner, no. 4686 (Herb. Univ. Calif., no. 207008), December.

Streblonema Porphyrae is an exceedingly diminutive, though apparently distinct, species, confined, so far as we know at present, to the cushion-like bases of *Porphyra naiadum*. It ramifies deep into the tissue, apparently not entering the cells.

Streblonema myrionematoides sp. nov.

Plate 44, figure 7

Frondibus microscopicis; partibus prostratis exiguissime evolvatis, inter strata duo aut tria externa cellularum hospitis leviter penetrantibus; filamentis erectis plus minusve ad superficiem hospitis fasciculato-ramosis; 65–80μ longis, plerumque fructuosis, pilis exiguis; cellulis filamentorum penetrantium 4–5μ diam., forma irregularibus; zoosporangiis ignotis; gametangiis numerosis, cylindricis, 50–65μ longis, 4.5–6.5μ latis; loculis uniseriatis.

Growing on the blade of *Laminaria Andersonii*. Moss Beach, San Mateo County, California. Type, Gardner, no. 4622 (Herb. Univ. Calif., no. 207005), July.

It is an extremely perplexing problem to decide upon the generic position of forms such as the one we have named and described above. It has close affinities with the three genera, *Streblonema*, *Ectocarpus*, and *Myrionema*. The erect fronds exterior to the host and more or less branched, with relatively scanty attaching portions, constitute the

vegetative portion of an *Ectocarpus* of microscopic size. The gametangia are strictly those of a typical *Myrionema*, but it lacks the disk-shaped basal layer of filaments spreading out on the surface of the host, characteristic of that genus. The extremely reduced character of the penetrating portion does not speak well for the genus *Streblonema*. On the whole, we feel that with our present criteria for these genera it best agrees with the characters of the genus *Streblonema*, where we are placing it. It penetrates the uninjured host, but only to a slight depth. The plants, however, are usually so congested that their growth soon crowds the surface layer of the host cells to such an extent that they die and disintegrate, there being no evidence that the associate penetrates them and absorbs their material. The palisade-like stratum of gametangia suggests very strongly the *Myrionema* character which is the reason for the specific name.

Streblonema penetrale sp. nov.

Plate 44, figures 3, 4

Frondibus stratum continuum pulvinatumque forma magnitudineque indefinitum supra stipitem hospitis formantibus; parte penetrante, filamentis parce ramosis in hospitem comparate profundi penetrantibus et ad superficiem hospitis perpendicularibus composita; filamentis erectis ad superficiem hospitis fasciculato-ramosis, 70–125μ longis, supra leviter attenuatis, non piliferis; cellulis filamentorum penetrantium cylindricis ad irregularibus, 6.5–8μ diam., 3–5-plo longioribus; cellulis filamentorum erectorum cylindricis ad leviter doliiformibus, 6.5–8μ diam., 1.5–2.5-plo longioribus; chromatophoris taeniatis; zoosporangiis ignotis; gametangiis cylindricis usque ad obtuse-fusiformibus, plus minusve irregularibus, 30–40μ longis, 8–11μ latis; loculis uniseriatis.

Growing on the stipes of *Hesperophycus Harveyanus*. Pacific Grove, California. Type, Gardner, no. 4677 (Herb. Univ. Calif., no. 207007), December.

Streblonema penetrale, like *S. myrionematoides* above, is a difficult species to classify. In its method of development and general structure it approximates to *S. myrionematoides* closely. The penetrating portion is much more highly developed than in that species, extending into the host among the cells to a depth of four or five times as great as the part which extends beyond the surface. The size of all the parts is, in general, greater than in *S. myrionematoides*. No horizontal filaments are present. The penetrating filaments are mostly perpendicular to the surface.

Streblonema vorax, sp. nov.

Plate 44, figures 1, 2

Frondibus microscopicis, filamentis prostratis profuse ramosis, maxime tortuosis, inter cellulas epidermales hospitis penetrantibus, in interiore hospitis diffundentibus et cellularum parenchymaticarum parietes dissolventibus, easdem complentibus, et earum partem interiorem devorantibus; cellulis 6–10μ longis, 5–8μ latis; filamentis erectis 400–600μ longis, 6.5–8μ diam., superne in pilis attenuatis, ad aut prope superficiem hospitis fasciculato-ramosis, massam compactam cellularum formantibus; zoosporangiis late clavatis, 60–100μ longis, 15–30μ latis; gametangiis numerosis, lateralibus, sessilibus aut pedicellis brevibus suffultis, anguste cylindricis, obtusis, 40–70μ (ad 100μ) longis, 7–9μ latis; loculis plerumque uniseriatis.

Growing on the outer ends of the leaves of eel-grass, in the lower littoral and upper sublittoral belts. Sitka, Alaska. Type, Gardner, no. 3968*b* (Herb. Univ. Calif., no. 207003), July.

Of all the species of *Streblonema* thus far discovered on our coast, *S. vorax* is the most destructive to the host. Although the penetrating filaments have abundance of chromatophores, the plants seem to be in a large degree parasitic. The cells of the host are closely compacted, and have thick walls, yet they are devoured in large quantities. We suggest the possibility of the secretion of enzymes with digestive power which act upon the cell wall and its protoplasm, after which they are absorbed. This plant is found in company with several other small Melanophyceae, Chlorophyceae, and Rhodophyceae, none of which penetrate the host.

Streblomena scabiosum sp. nov.

Plate 44, figure 5

Frondibus pustulas rotundas aut ellipticas magnitudine indefinatas in superficie hospitis formantibus; partibus penetrantibus filamentis copiose ramosis primo inter cellulas penetrantibus et eas necantibus, ultimo interiorem cellularum occupantibus et eversionem totam efficientibus; filamentis erectis supra superficiem hospitis extendentibus, aut simplicibus aut plus minusve basi fasciculato-ramosis, 50–80μ altis; cellulis filamentorum repentium forma magnitudineque maxime irregularibus; cellulis filamentorum erectorum cylindricis, 4.5–5.5μ diam., 1–2.5-plo longioribus; chromatophoris taeniatis; zoosporangiis ignotis; gametangiis cylindricis, sessilibus aut brevi-pedicellatis, supra superficiem hospitis extendentibus, 40–60μ longis, 4.5–6μ latis.

Growing on the stipe of *Nereocystis Luetkeana*. Cast ashore near the "Cliff House," San Francisco, California. Type, Gardner, no. 4628 (Herb. Univ. Calif., no. 207006), August.

Streblonema scabiosum forms marked scrofulous-like areas on the lower part of the stipe of the host. It has a disastrous effect upon the host, destroying its cells as far as it penetrates, and seems constantly to spread by new infections around the margin of the affected area. The cause of the death of the cells of the host has not been investigated. In habit of growth and general form the species seems related to *S. myrionematoides* and to *S. penetrale*.

Streblonema evagatum sp. nov.

Plate 42, figures 1–5

Frondibus maculas orbiculares 1–2 cm. diam. formantibus; filamentis repentibus irregularibus, multe ramosis, inter bases sporangiorum hospitis penetrantibus; filamentis erectis fasciculato-ramosis, plerumque in hospite submersis, ad apicem basimque levissime attenuatis, 190–230μ altis; cellulis filamentorum repentium 3.5–4μ diam.; cellulis filamentorum erectorum basim 4μ diam., 2–3.5-plo longioribus, in parte latissimo 6.5–7.5μ diam., 1–2-plo longioribus, cylindricis, ad dissepimenta leviter constrictis; chromatophoris taeniatis, in cellula quaque 1–2; zoosporangiis ignotis; gametangiis numerosis, cylindricis, lateralibus, sessilibus aut in pedicellis curtis suffultis, 65–80μ longis, 5.5–6.5μ latis; loculis uniseriatis.

Growing in the blades of *Laminaria Andersonii*, upper sublittoral belt. Cypress Point, Monterey County, California. Type, Gardner no. 4688 (Herb. Univ. Calif., no. 207009), December.

This species has a habit of growth very similar to that of *Streblonema pacificum*, but the plants cover much more extensive areas which are quite certainly not infested by a single plant, as may be the case in that species. Their presence seems to affect the host materially, to a large extent destroying its sporangia and causing discoloration. It is possibly partially parasitic.

Streblonema rugosum sp. nov.

Plate 43, figures 5–7

Frondibus microscopicis in superficie hospitis areas rugosas extensas efficientibus; filamentis repentibus inter cellulas superficiales hospitis penetrantibus et filamenta erecta, fasciculato-ramosa, fructifera et pilifera emittentibus; cellulis filamentorum et erectorum et repentium forma magnitudineque irregularibus; chromatophoris taeniatis; zoosporangiis ignotis; gametangiis obtuse fusiformibus, in filamentis erectis plurimis terminalibus, 18–24μ longis, 5–6.5μ latis; loculi uniseriatis, in serie longitudinali quaque 4–6.

Growing on the blade of *Alaria tenuifolia.* Friday Harbor, Washington. Type, Gardner, no. 4041 (Herb. Univ. Calif., no. 207004), July.

This species, like *Streblonema myrionematoides* and *S. scabiosum,* has the larger part outside of the host. It penetrates to a considerable depth among the cells of the uninjured host, later apparently mechanically causing the death of a few surface cells and an abnormal growth of others, giving to the surface a rugose appearance. The plants seem to associate in small groups of indefinite shape and size, often confluent and, although small, can readily be detected by the peculiar appearance they give to the host.

Streblonema transfixum sp. nov.

Frondibus maculas 5–8 mm. diam. formantibus; filamentis repentibus inter cellulas hospitis profunde penetrantibus, distortis, irregulariter ramosis, 4–5μ diam., filamenta dispersa, curta erecta, eramosa, e superficie hospitis protusa et a gametangiis terminata emittentibus; cellulis filamentorum erectorum cylindricis, 7–9μ diam., 0.75–1.5-plo longioribus; chromatophoris taeniatis, parietem cellulae proxime tegentibus; zoosporangiis ignotis; gametangiis cylindrico-conicis, obtusis, 40–60μ longis, 8–12μ latis; loculis 1–2-seriate.

Growing on *Desmarestia ligulata* f. *herbacea.* San Pedro, California. Type, Gardner, no. 1992a (Herb. Univ. Calif., no. 207001), September.

Streblonema transfixum, here described, forms definite, discolored areas on the surface of the host, readily detectable. The species is described from dried material. The cells of the host are much collapsed and do not straighten out when soaked and boiled, hence the details of the species are not so thoroughly and satisfactorily presented as is desirable. The plants penetrate among the cells of the host and seemingly pass clear through it. Just how much constitutes a single plant cannot at present be made out.

Streblonema corymbiferum sp. nov.

Plate 43, figure 8

Frondibus microscopicis, filamentis irregulariter alterne ramosis et inter cellulis hospitis penetrantibus compositis, ramulis fructiferis plane aggregatis, fasciculos corymbiformes prope superficiem hospitis formantibus; cellulis plerumque cylindricis, pro parte irregularibus, 4–5μ diam., 1.5–4-plo longioribus; chromatophoris taeniatis, parietem cellulae non tegentibus; zoosporangiis ignotis; gametangiis cylindricis

usque ad leviter fusiformibus, obtusis, in pedicellis curtis suffultis aggregatis aut in filamentis repentibus prope superficiem hospitis sessilibus, 25–35μ longis, 4.5–5.5μ latis; loculis uniseriatis, septis plerumque obliquis.

Growing on *Cumagloia Andersonii* (Farlow) S. and G., in company with *Streblonema anomalum* and *S. Johnstonae*. San Pedro, California. Type, Mrs. H. D. Johnston, no. 115*a* (Herb. Univ. Calif., no. 94663), August.

While studying the material of *Nemalion Andersonii* Farlow, collected by Mrs. H. D. Johnston at San Pedro, California, in 1899 and deposited in the Herbarium of the University of California under no. 94663, some specimens of Ectocarpaceae were incidentally observed. When we came to study our material of this family, these specimens were given careful scrutiny with the result that three species new to science were detected on a single specimen of the host, viz., *Streblonema corymbiferum*, *S. anomalum*, and *S. Johnstonae*, all of which are presented for the first time in this paper.

The habit of each and the size of all the parts are so characteristic that, notwithstanding their intimate association on the same host, they can readily be distinguished. *S. corymbiferum* is the most delicate of the three. The very frequent grouping of the gametangia into corymb-like clusters is one of the most prominent distinguishing characters of the species. Other species of this genus are as small or even smaller. In size of parts, somewhat in habit and in habitat, it resembles *S. minutissimum* Saunders, found growing at Sitka, Alaska, on "*Lichmannia* sp." (Saunders, 1901, p. 416).

Streblonema anomalum sp. nov.

Plate 43, figures 1–3

Frondibus microscopicis, plus minusve confluentibus; filamentis partis prostratae inter cellulas hospitis penetrantibus moderate et irregulariter ramosis, multe contortis, usque ad 16μ diam.; filamentis erectis simplicibus, plerumque cylindricis, pro parte obtusis et pro parte piliferis, 200–250μ longis, ultra superficiem hospitis extendentibus; filamentis piliferis sparsis, e filamentis repentibus oriundis; cellulis filamentorum repentium plus minusve in partibus senilibus 1–2-plo longitudinaliter divisis, filamentum polysiphoneum producentibus, 18–24μ diam.; cellulis alteris forma leviter irregularibus, 8–11μ diam., admodum ad dissepimenta leviter constrictis; cellulis filamentorum erectorum cylindricis, 8–9μ diam., quadratis; chromatophoris singulis, taeniatis, in filamentis erectis continuis, in filamentis repentibus plus minusve interruptis; zoosporangiis ellipsoideis, ovoideis

aut proxime sphaericis, 40–60μ longis, 28–35μ latis, in filamentis repentibus sessilibus; gametangiis cylindrico-conicis, plerumque obtusis, 50–100μ longis, 10–16μ latis, sessilibus aut in filamentis repentibus longe-pedicellatis singulis aut secundis.

Growing in *Cumagloia Andersonii* (Farlow) S. and G. in company with *Streblonema corymbiferum* and *S. Johnstonae*. San Pedro, California. Type, Mrs. H. D. Johnston, no. 115*b* (Herb. Univ. Calif., no. 94663), August.

Streblonema fasciculatum Saunders, Phyc. Mem., 1898, p. 148 (not of Thuret).

Examination of a small piece of authentic material of *S. fasciculatum* Saunders collected at San Pedro, California, in August, 1896, revealed the presence of specimens of the same three species mentioned under *S. corymbiferum* of this paper, collected by Mrs. Johnston at the same place and in the same month. *S. anomalum* is undoubtedly the one to which Saunders refers as *S. fasciculatum* Thuret. It does not seem, however, to be this species, if we have a correct conception of what *S. fasciculatum* Thuret includes. This species was published in Le Jolis, Algues marines de Cherbourg, no. 100, and in Liste, 1863, p. 73. Thuret quotes as a synonym, *S. volubilis* Pringsheim (Beitr. Morph. Meeres Alg., p. 13, plate 3, fig. B, read in 1862). Pringsheim's figure of *volubilis* shows the gametangia fasciculately branched, and he states that this character is one of the chief characters of the genus *Streblonema*. This figure has been much quoted since. He gives no measurements of the parts, neither does Thuret.

Reinke (Algenfl., 1889, p. 41) recognizes *Streblonema* as a subgenus of *Ectocarpus*. He recognizes Pringsheim's plant, quoting the above figure, but since *volubilis* was already occupied by Crouan (1867, p. 161) and *fasciculatum* was occupied by Harvey (Phyc. Brit., pl. 273), he renamed the plant, calling it *Pringsheimii*. Hauck (1884, p. 323) seems to have been the first to give measurements of the various parts of the plant. He lists it under *Streblonema*, cites the above literature of Thuret, and quotes *S. volubilis* Pringsheim. Considering Pringsheim's plant, recognized by Reinke and Hauck, as being the same as Thuret's, and taking Pringsheim's figure and Hauck's measurements as being correct for Thuret's *S. fasciculatum*, then our plant is distinct and undescribed.

There is a little doubt at present in our minds whether the plant we are here describing as *Streblonema anomalum* is one or two species. We do not find the filaments bearing the zoosporangia in the type

material examined to be like those figured by Saunders. His figures show the main filaments as being like those of all the known *Streblonemas*, monosiphonous, while those in both collections of material which we have examined are uniformly polysiphonous, that is, the cells of the main central parts of the thallus are all divided once or twice lengthwise. This never takes place in the plants which bear gametangia and which are intimately associated with them.

The measurements, method of branching of the two sets of plants, and their chromatophore characters are practically the same. At least two interpretations of this polysiphonous phenomenon appeal to us. They may represent a polymorphic state, in which a nonsexual plant differs in form from a sexual plant of the same species, a unique condition in the genus *Streblonema*, or the polysiphonous condition of the main filaments, found only in the nonsexual plants, may represent a character belonging to a wholly different genus, and hence it is a new species of that genus. Until a more extensive study of fresh material can be made, we feel that it is best to take the former view, and place it in a new and polymorphic species of *Streblonema*. We have amended the family Ectocarpaceae to include species with this polysiphonous condition.

Streblonema Johnstonae sp. nov.

Plate 43, figure 4

Frondibus microscopicis; filamentis repentibus moderate ramosis, ramis alternis aut oppositis, raro leviter secundis; filamentis erectis plerumque simplicibus, apice basimque leviter attenuatis, supra superficiem hospitis extendentibus, pro parte, brevi-piliferis; cellulis filamentorum primariorum repentium forma plus minusve variabilibus, plerumque doliiformibus, 12–18μ diam., 2.5–5-plo longioribus; cellulis filamentorum erectorum pro parte latissima usque ad 24μ diam., fere cylindricis, ad dissepimenta constrictis; chromatophoris tenuibus, parietalibus, in cellula quaque singulis, parietes cellularum fere tegentibus; zoosporangiis ignotis; gametangiis conicis usque ad inaequaliter fusiformibus, 90–130μ longis, 28–36μ latis, plerumque brevipediccllatis in filamentis prope superficiem hospitis repentibus positis.

Growing in *Cumagloia Andersonii* (Farlow) S. and G. in company with *Streblonema corymbiferum* and *S. anomalum*. San Pedro, California. Type, Mrs. H. D. Johnston, no. 115*c* (Herb. Univ. Calif., no. 94663), August.

Of the three plants found ramifying among the filaments of the host mentioned above, *Streblonema Johnstonae* is the most robust in all

of its parts. It can readily be distinguished from the other two species with which it is associated by the large size of the gametangia. No zoosporangia have been observed. We take pleasure in dedicating this species to Mrs. H. D. Johnston, who collected the host and donated it to the Herbarium of the University of California with several other interesting forms from San Pedro, California.

Streblonema aecidioides f. **pacificum** forma nov.

Plate 44, figures 8, 9

Frondibus microscopicis, supra superficiem hospitis ut maculas elevatas 75–150μ diam. notatis; parte vegetativa stratum plus minusve parenchymaticum exigue infra stratum superficiale hospitis positum et infra filamenta pauca radiciformia in hospitem profundiore penetrantia emittens formantibus; filamentis erectis omnibus fructiferis filamentis paucis, piliferis in centro frondis positis exceptis; cellulis filamentorum piliferorum 4–5.5μ diam., inferne quadratis, superne 5–8-plo longioribus, evaginatis; zoosporangiis(?) anguste clavatis, sessilibus, 22–28μ longis, apice 8–12μ latis; gametangiis numerosis, dense aggregatis, cylindricis, in strato prostrato sessilibus, 45–55μ longis, 5–6.5μ latis; loculis uniseriatis.

Growing within the lamina of *Hedophyllum sessile* (Aresch.) Setchell, near the outer end. Neah Bay, Washington. Type, Gardner, no. 3866*a* (Herb. Univ. Calif., no. 207002), May.

Streblonema aecidioides f. *pacificum* seems very closely related to the *Ectocarpus aecidioides* of Rosenvinge (1893, p. 894), found growing in Greenland on *Laminaria longicruris and L. Groenlandica*. It differs only in minor details as to the dimensions of the parts. Regarding the zoosporangia we have to speak with uncertainty. As figured by Rosenvinge, the Greenland plant has them well developed and producing zoospores. They are in distinct "aecidia" and apparently on distinct nonsexual plants. In our species they likewise appear to be on nonsexual plants. In ours there is no indication of the production of zoospores. They are possibly too young, or possibly they are abortive organs so commonly met with in various other genera on our coast, the nature of which is still an open question. This form seems to enter the host from the surface and after penetrating to the second layer of cells spreads out horizontally between the surface layer and the second layer. Later, filaments arise from the under side of this layer and penetrate among the cells of the host, apparently never entering them. Finally from the upper surface each cell in the central region of the layer gives rise to a filament and the mass acting together

lifts up the surface layer of cells of the host, forming a small blister which finally ruptures, as in the case of Rosenvinge's plants. The erect filaments are almost simultaneously transformed into gametangia, except a few in the center which develop into hairs.

Foslie (1894, p. 167, 23 in reprint) describes forms of the same species found growing on *Laminaria saccharina* at Kjelvik and at Lyngo near Tromso, Norway. These he listed under *Ectocarpus* (*Streblonema*) *accidioides* Rosenvinge. The measurements of the parts of his forms average, in general, a little larger than those of Rosenvinge. De-Toni (1895, p. 577) cites these Arctic plants under *Streblonema accidioides* Rosenv. Foslie gives 80μ as the extreme length of the gametangia.

Streblonema investiens (Collins) comb. nov.

Fronds occupying indefinite areas on the host; creeping filaments irregularly branched, often curving outward and bearing on the outside short, simple, or sparsely branched filaments; hairs sparse; cells of creeping filaments 5–8μ diam., 1–2 (up to 4) times as long, swollen, or cylindrical; cells of the ramuli 6μ diam., 1–2 times as long; cells of the hairs 8μ diam.; chromatophores discoid, small, several in a cell; zoosporangia ovoid, sessile or on 1-celled pedicels on both the creeping filaments and the ramuli, 20μ long, 15μ broad; gametangia cylindrical, 25–40μ long, 8–10μ broad; loculi mostly uniseriate, gametangia and zoosporangia growing on the same plant.

Growing in the fronds of *Helminthocladia calvadosii* (Lamour.) Setchell. San Pedro, California. July.

Stropsithalia investiens Collins, *in* Collins, Holden, and Setchell, Phyc. Bor.-Amer. (Exsicc), no. 738.

It seems that the chief distinction between the genera *Stropsithalia* Sauvageau and *Streblonema* Derb. and Sol. is the secretion by *Stropsithalia* of a rather copious gelatinous sheath investing the entire plant, particularly the exposed portions, the ramuli. Since we are not able to demonstrate the presence of such a sheath, even to the slightest degree, we have thought it best to place Collins' *Stropsithalia investiens* in the genus *Streblonema*.

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PLATE 42

Streblonema evagatum S. and G.

Figs. 1, 2, 4. Fragments of plants freed from their host. × 250.

Fig. 3. A diagrammatic section.

Fig. 5. A young plant penetrating among the sporangia of the host. × 125.

Pylaiella unilateralis S. and G.

Fig. 6. Diagrammatic sketch of a small group of plants.

Fig. 7. A filament showing method of branching and characteristic intercalary zoosporangia. × 125.

Fig. 8. A small fragment showing longitudinal divisions of the cells of the main filament in the region of branching. × 250.

Pylaiella tenella S. and G.

Fig. 9. A fragment of a filament showing gametangia, and a fragment to the right of it showing chromatophores. × 500.

Fig. 10. A fragment showing zoosporangia. × 500.

Fig. 11. A fragment showing seriate intercalary gametangia. × 125.

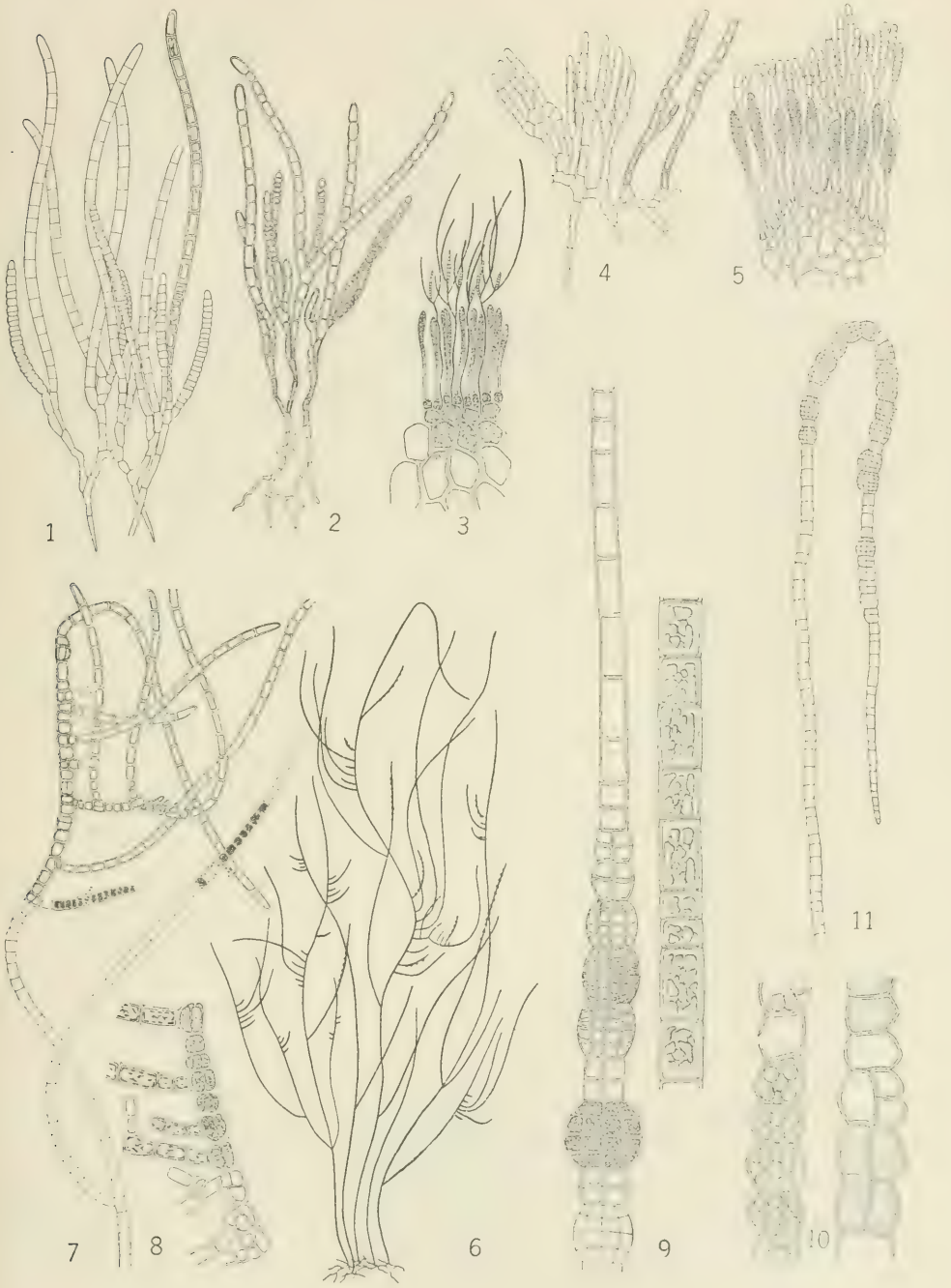
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PLATE 43

Streblonema anomalum S. and G.

Fig. 1. A part of a plant freed from its host bearing gametangia. × 250.

Figs. 2, 3. Fragments of plants bearing zoosporangia, some of which contain mature zoospores. The cells of the main filaments are divided longitudinally. × 250.

Streblonema Johnstonae S. and G.

Fig. 4. Parts of plants showing characteristic creeping and erect filaments and gametangia. × 125.

Streblonema rugosum S. and G.

Fig. 5. Section through the host perpendicular to its surface, showing the papillate character caused by the presence of *Streblonema*. Diagrammatic.

Fig. 6. A surface view of figure 5. Diagrammatic.

Fig. 7. A section showing the structure of the *Streblonema* plants and their relation to the host. × 250.

Streblonema corymbiferum S. and G.

Fig. 8. Fragments of typical plants freed from their host. × 250.

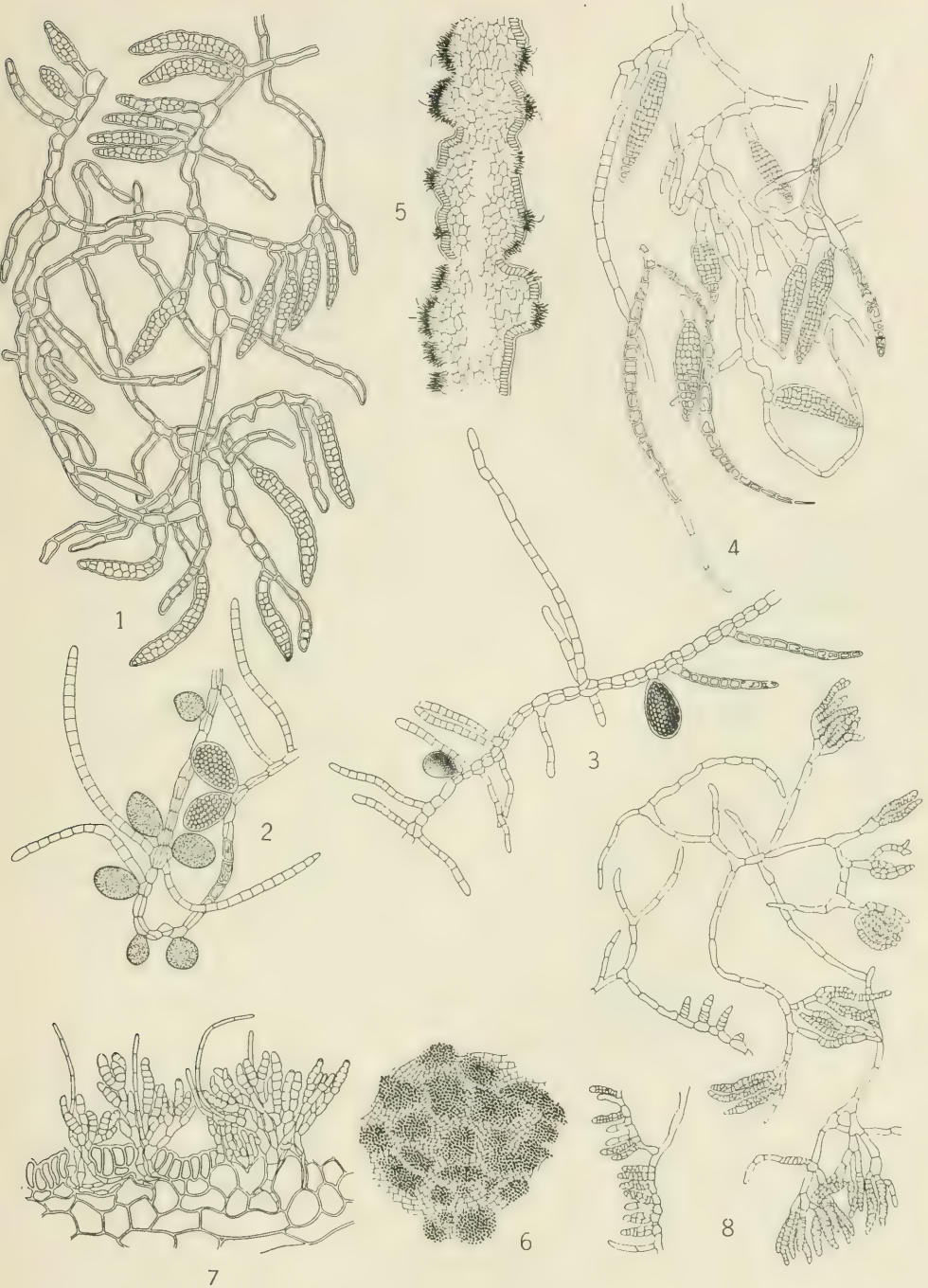
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PLATE 44

Streblonema vorax S. and G.

Fig. 1. A section through the host showing the presence of the parasite and its effect upon the host. × 125.

Fig. 2. A fragment of a plant showing the tortuous creeping filament, a true hair, and several typical gametangia. × 125.

Streblonema penetrale S. and G.

Fig. 3. A section through the host perpendicular to its surface showing the apparent disorganizing effect of the penetrating portion of the *Streblonema*. × 125.

Fig. 4. Individual plants separated from the host. × 250.

Streblonema scabiosum S. and G.

Fig. 5. A section through the host perpendicular to its surface showing the relation of the two plants. × 250.

Streblonema Porphyrae S. and G.

Fig. 6. A section showing the relation of this *Streblonema* to its host. × 125.

Streblonema myrionematoides S. and G.

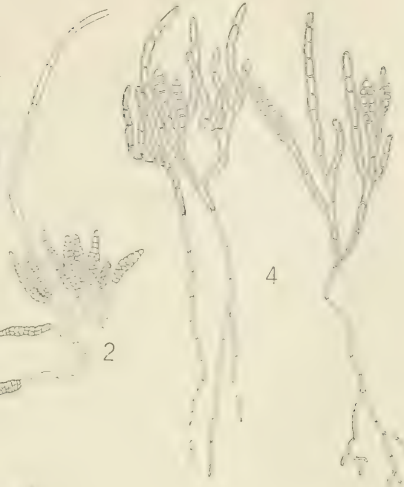
Fig. 7. Showing plants in various stages of development. × 250.

Streblonema aecidioides f. *pacificum* S. and G.

Fig. 8. A section through an "aecidium" and perpendicular to the surface of the host, showing the structure and relations of the two plants. The section seemingly represents young zoosporangia. × 250.

Fig. 9. The same as figure 8, but of a plant bearing gametangia. × 250.

1



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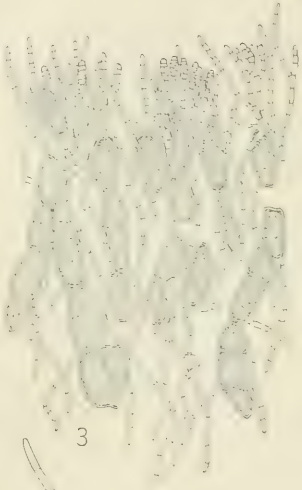

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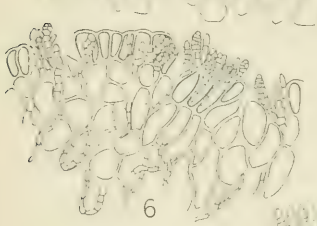

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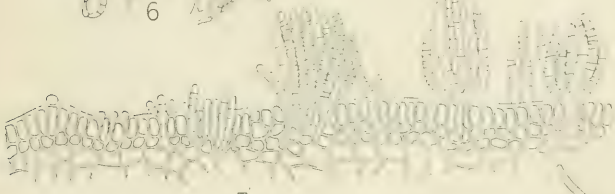

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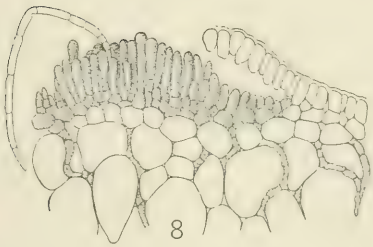

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VI. NEW SPECIES OF ECTOCARPUS

Since the publication of our account of the Algae of Northwestern America (1903), more or less extensive search and study has been carried on in that same region as well as farther south along the whole coast of North America, with the result that a considerable number of forms of Ectocarpus have been discovered and much more data on previously known forms have been brought to light, necessitating some changes in our previous account and particularly necessitating the founding of several new and quite distinct species. We do not imagine that the field has been, by any means, thoroughly investigated, but we are publishing these findings up to date hoping to stimulate further investigation. Doubtless there are many more undiscovered species and certainly much remains to be worked out regarding life-histories of the various known species. The "megasporangia," "meiosporangia," and "antheridia" of Sauvageau (1896, 1896*a*, 1896*b*, 1896*c*) offer further and attractive subjects for investigation in the reproductive phase of this group. The nature of the "zoosporangia" or "unilocular sporangia" and the position of the plants which bear them in the life cycle is a matter concerning which but little is known, and which deserves critical study.

For the sake of uniformity in the method of grouping, in our Pacific coast algological studies, we have found it necessary to name a new Order for use in our forthcoming Part III, the Melanophyceae, of our 'Marine Algae of the Pacific Coast of North America." The following diagnosis, here published for the first time, sets forth our conception of the group.

Ectocarpales nom. nov.

Confervoid (monosiphonous) or solid Phaeosporeae of varying dimensions, habit, and complexity, typically possessing unilocular zoosporangia and plurilocular gametangia and with no portion of the cell membranes turning black with *eau de Javelle;* growth in length strictly apical, subapical ("trichothallic"), or more or less intermediate between typical forms of either; both unilocular zoosporangia and plurilocular gametangia rarely on the same individual in some species, but, most commonly, borne on different individuals, thus pointing to an alternation of generations, reduction division taking place in the primary nucleus of the unilocular zoosporangia, at least in some species; gametophyte and sporophyte practically indistinguishable as to size and complexity.

Ectocarpaceae Oltmanns, Morph. und Biol. der Alg., vol. 1, 1904, p. 350 (pro parte majore).

It seems more consistent with the present usage in other subclasses of the Thallophyta, to consider the extended Ectocarpaceae of Oltmanns as an Order rather than as a Family. While the families under it present a very considerable variety in the details of structural differences, they have in common the possession of plurilocular gametangia and an identity in size and structure of both gametophyte and sporophyte. The Ectocarpales are closely related to the Cutleriales, but in the latter there are some decided differences between the two generations. From the Sphacelariales, the Ectocarpales differ in the absence of the conspicuous apical cell and the very different cell wall. The cell wall, or the older layers of it, changes to black in the Sphacelariales when treated with *eau de Javelle*, but does not show this reaction in any of the Ectocarpales. The Laminariales are to be distinguished from all the other orders of the Phaeosporeae by their intercalary region of longitudinal growth in connection with their microscopic gametophyte. The existence of a reduced gametophyte in the Dictyosiphonales separates them also from the Ectocarpales.

Ectocarpus acutus nom. nov.

Plate 48, figures 36–39, and Plate 49, figures 40, 41

Frondibus 5–9 cm. altis, siccitate saturate fuscis, vivo olivario-viridibus, plumosis; filamentis erectis, inferne plus minusve intricatis fasciculatisque, superne liberis, profuse ramosis, filamentis primariis corticatis; ramis plerumque alternis, strictis; ramulis ultimis plerumque secundis, acute subulatis; cellulis leviter doliiformibus, 40–60μ diam., 0.4–2-plo longioribus quam latis (vulgo brevioribus quam latis); chromatophoris crassis, irregulariter ramosis, in cellula quaque paucis, pyrenoideas (plures) exhibentibus; zoosporangiis ignotis; gametangiis numerosis et regulariter dispositis, cylindrico-conicis, 100–150μ (usque ad 230μ) longis, 20–35μ latis.

Growing, for the most part at least, on larger Melanophyceae. Puget Sound to central California (Carmel).

Ectocarpus penicillatus Saunders, Phyc. Mem., 1889, p. 155, pl. 21, figs. 3, 4 (not of Kjellm.). *Ectocarpus confervoides* f. *acuminatus* Collins, *in* Setchell and Gardner, Alg. N.W. Amer., 1903, p. 237, Mar. Alg. Vancouver Is., 1913, p. 106; Collins, Holden, and Setchell, Phyc. Bor.-Amer. (Exsicc.), nos. 1033, 1127.

The type of the species is no. 2886, Gardner (Herb. Univ. Calif., no. 206991), collected at Carmel, California, in May, 1915, and grow-

ing on a form of "*Desmarestia ligulata.*" It seems to be the same as the plant figured (and described) by Saunders (*loc. cit.*) under *Ectocarpus penicillatus.* It is undoubtedly the same plant as that described by F. S. Collins under the name *E. confervoides* f. *acuminatus* which was founded on no. 235, Gardner (Herb. Univ. Calif., no. 99022) collected at Whidby Island, Washington, growing on a broad form of *Desmarestia.* Its affinities are closely with *Ectocarpus confervoides* f. *typicus*, but it has shorter cells, sharper ramuli, decidedly constricted filaments, with the gametangia more inclined toward cylindrical than is general in that form. The chromatophores are more distinctly band-shaped and more separated from one another than in *E. confervoides.*

A few small but profusely fruiting specimens of plants seemingly of this species have been found growing on *Mesogloia Andersonii* at Neah Bay, Washington (Gardner, no. 3817). These were attached to the host by means of penetrating rhizoidal filaments, particularly by the descending corticating filaments. The specimens differ from the typical form in that they are smaller, the gametangia are shorter and blunter, and on separate individuals occur seriate zoosporangia(?), some of which are divided longitudinally into four loculi. Further study of more material will be necessary to determine the status of this form. For the present we are placing it with *E. acutus.* The gametangia are represented on plate 49, figure 41, and the zoosporangia on plate 49, figure 40. The zoosporangia are very numerous, and they resemble in form those figured by Sauvageau (1896*b*, p. 33, reprint) for *Ectocarpus virescens.* They, however, have a glistening appearance, as though they were abortive or in a pathological condition, while those represented by Sauvageau are producing zoospores. This condition in which we find ours is quite common among our Pacific Coast species of *Ectocarpus.* We have not yet seen a single specimen in which the so-called seriate zoosporangia show any indication of producing zoospores.

Ectocarpus affinis sp. nov.

Plate 46, figures 16, 17

Frondibus minutissimis, 500–700μ altis, ad hospitem per filamenta rhizoidea pauca ramosa, decolorata, implicata affixis; filamentis erectis sparse ramosis, superne longe attenuatis, piliferis; ramis alternis aut oppositis; cellulis filamentorum primariorum cylindricis, basim 24–30μ diam., apice 9–11μ, in longitudine per filamentum totum variabilibus, 0.75–3-plo longioribus quam latis; chromatophoris parvis, tenuibus, in

cellulis juvenis, angulato-laminaeformibus, in cellulis vetustioribus fere regulariter discoideis; zoosporangiis ignotis; gametangiis lateralibus, plerumque sessilibus, interdum 1-cellulato pedicellatis, solitariis, secundis aut ad cellulam singulam verticillatis, obtuse-conicis usque ad sphaeroideis, 28–31μ longis, 25–28μ latis, per filamentum totam usque ad pilos terminales seriatis.

Growing on *Callithamnion* sp. Sitka, Alaska. Type, Gardner, no. 3961 (Herb. Univ. Calif., no. 206998), July.

Two collections from Sitka, Alaska, but both made on the same day, show a small *Ectocarpus* growing on a species of *Callithamnion* which is so closely related to *E. ovatus* Kjellman (1877, p. 35) that perhaps it may seem necessary at some time to refer it to that species. The plants are, however, less stout than those of Kjellman and with more nearly spherical gametangia. For these reasons and because of its geographic remoteness and the somewhat different climatic conditions, we feel that it is desirable to describe the Alaskan plant as a distinct, but closely related species.

Ectocarpus chantransioides sp. nov.

Plate 48, figures 28–31

Frondibus e filamentis contortis repentibusque oriendis, pulvinulos densos hemisphaericosque, 4–8 mm. altos formantibus; ramis profusis, inferne alternis, superne plerumque secundis; filamentis primariis ramisque non attenuatis, apice crescentibus;; cellulis 8–10μ diam., inferne 2–3-plo longioribus quam latis, superne quadratis; chromatophoris taeniatis; zoosporangiis ignotis; gametangiis plerumque sessilibus, aut brevi pedicellatis, anguste cylindrico-conicis, 80–110μ longis, basim 16–20μ latis.

Growing on boulders in the lower littoral belt. Three miles northwest of Santa Monica, California. Type, Gardner, no. 2523 (Herb. Univ. Calif., no. 206988), November.

The habit of *Ectocarpus chantransioides* distinguishes it at once from all other species of the genus with the exception of *E. hemisphericus* Saunders. The latter species is always found, so far as our knowledge is concerned, epiphytic on Fucaceae, while the former species is confined to rocks. *Ectocarpus chantransioides* has also more slender filaments than has *E. hemisphericus*, not at all tapering, and has distinct apical growth. The gametangia are differently shaped, being longer and more slender. It is therefore very distinct even from *E. hemisphericus*. It resembles the genus *Choristocarpus* of the family Choristocarpaceae, as diagnosed by Kjellman (1897, pp. 190, 191), in

having apical growth. The growth in length of the erect filaments in Choristocarpaceae is by the division of the terminal cell only, whereas in *E. chantransioides* the meristem extends over a number of cells at the outer or apical end of the filaments. These cells, some 10 to 15 in number, are much richer in cell contents, the terminal cell being the richest of all in the series. This is a very unusual condition for an *Ectocarpus*. The nearly uniform diameter throughout of the erect filaments and their method of branching resemble to a remarkable degree those characters found in *Chantransia*. The gametangia are typically those of *Ectocarpus*, and notwithstanding the other rather unusual characters, it seems to be most closely related to that genus, but a very distinct species.

Ectocarpus commensalis sp. nov.

Plate 48, figures 32–35

Frondibus 200–400μ altis, dense fasciculatis, per filamenta rhizoidea intricata, parce ramosa inter utriculos et usque inter filamenta medullaria hospitis penetrantia affixis; filamentis erectis prope basim alterne ramosis, superne simplicibus et leviter attenuatis, non piliferis; cellulis filamentorum erectorum cylindricis, non constrictis, basim 12–18μ diam., 1.5–2.5-plo longioribus quam latis; chromatophoris taeniatis in cellula quaque paucis; zoosporangiis ignotis; gametangiis obtuse fusiformibus usque ad cylindrico-conicis, brevi-pedicellatis, prope basim filamentorum plerumque lateralibus, raro terminalibus, 60–100μ longis, 15–20μ latis.

Growing on *Codium Setchellii* Gardner, Carmel Bay, and on *Codium fragile* (Suringar) Hariot, Pacific Grove, Monterey County, California. Type, Gardner, no. 3319 (Herb. Univ. Calif., no. 206994), May.

This minute species is one of several occurring on species of *Codium*, both on this coast and on that of southwestern Europe. The colorless rhizoidal filaments descend into the substance of the host even to the central (or basal) medullary tissues. The smaller diameter of the erect filaments and the more narrowly conical or fusiform gametangia readily distinguish this species from the others.

Ectocarpus eramosus sp. nov.

Plate 47, figures 18–23

Frondibus diffusis aut flocculosis, 1–3 mm. altis, per filamenta rhizoidea irregulariter ramosa inter utriculos hospitis profunde penetrantes affixis; filamentis erectis eramosis aut raro ramos breves,

divergentes vulgo in gametangiis terminantes emittentibus, basim et apice leviter attenuatis, non piliferis; cellulis filamentorum maturorum 28–40μ diam., 0.5–1.25-plo longioribus quam latis, cylindricis, levissime constrictis; chromatophoris comparate crassis, dense confertis, irregulariter taeniatis, sine pyrenoideis; zoosporangiis ignotis; gametangiis maxime magnitudine formaque variabilibus aut lateralibus et per filamenta tota alternis aut interdum in filamentis primariis terminalibus et seriatis plerumque pedicellis pauciecllulatis, lateralibus cylindricis usque ad cylindrico-conicis, 150–230μ longis, 26–36μ latis, terminalibus seriatis, 700–900μ longis, 15–20μ latis.

Growing on *Codium fragile* in the lower littoral belt. Near the entrance to Tomales Bay, Marin County, California. Type, Gardner, no. 3448*b* (Herb. Univ. Calif., no. 206995), August.

This very small species has the general appearance of a form of *Ectocarpus confervoides*, but the cells are short and the filaments very slightly constricted at the partitions. It seems, in these respects, nearer to *E. acutus* and *E. corticulatus*, possibly bearing something of the same relation to these species that the dwarf forms of *E. confervoides* do to the typical form. *Ectocarpus cramosus*, however, is not readily to be referred as a dwarf form of either *E. acutus* or *E. corticulatus* and is consequently to be kept separate, at least for the present.

Ectocarpus flagelliferus sp. nov.

Plate 47, figures 25–27

Frondibus dense floccosis, 3–5 mm. altis, per filamenta pauca repentia et rhizoidea e cellulis inferis descendentia, decolorata affixis; filamentis erectis inferne simplicibus, superne sparse et alterne ramosis, superne longe attenuatis, inferne abrupte contractis, juvenis piliferis; cellulis filamentorum primariorum leviter doliiformibus, 25–35μ diam., 0.25–1.5-plo longioribus quam latis; chromatophoris parvis, irregulariter taeniatis aut laminaeformibus, pyrenoidis deuntibus; zoosporangiis ignotis; gametangiis magnitudine formaque variabilibus fusiformibus usque ad cylindrico-conicis, plerumque in pedicellis longis lateralibus, interdum in filamentis curtis erectisque terminalibus, aut in filamentis primariis longe-seriato-intercalaribus, lateralibus 125–200μ longis, 28–40μ latis, terminalibus et intercalaribus usque ad 1.5 mm. longis.

Growing on eel-grass. Sitka, Alaska. Type, Gardner, no. 3970 (Herb. Univ. Calif., no. 206999), July.

The species we have named *Ectocarpus flagelliferus*, while resembling superficially some of the shortest plants of *Ectocarpus confervoides* f. *variabilis*, presents several peculiarities which are characteristic. The plants of this species are attached, so far as the

adult specimens we have for study are concerned, by rhizoidal filaments which originate from several of the lower cells of the erect filaments and form complex basal masses which almost completely obscure the creeping filaments. Neither the rhizoidal filaments nor the creeping filaments, however, penetrate the host. The chromatophores are small and irregular in outline, seeming to be short bands rather than regular disks. They are generally so closely placed in the younger cells as to seem almost like a continuous band, but are separate in the older cells with slender processes almost connecting them to one another. The cells are short and the erect filaments and their branches extend out into long hairs like whip-lashes. The lateral gametangia are variable in shape, arranged much as in *Ectocarpus confervoides* f. *variabilis,* but are of different dimensions. Besides the characteristic *Ectocarpus*-type of gametangia which are lateral, there occur terminal seriate gametangia of the *Pylaiella*-type which reach an extreme length of 1.5 mm.

Ectocarpus flocculiformis sp. nov.

Plate 47, figure 24

Frondibus dense caespitosis, 0.75–1.5 mm. altis, per filamenta intertexta, penetrantia, rhizoidea affixis; filamentis erectis basi plus minusve furcatis, superne simplicibus aut in plantis, maximis, ramulis paucis, curtis, alternisque instructis, basi leviter attenuatis, superne longe attenuatis, non piliferis; cellulis cylindricis ad leviter doliiformibus, 20–25μ diam., 1–2.5-plo longioribus quam latis; chromatophoris numerosis, in cellulis junioribus angulato-discoideis, in vetustioribus rotundatis; zoosporangiis ellipsoideis, 56–66μ longis, 35–40μ latis, prope basim filamentorum erectorum in pedicellis curtis suffultis; gametangiis ovoideis ad ellipsoideis, numerosis, sessilibus aut brevi-pedicellatis, prope basim filamentorum erectorum lateralibus, 95–110μ (usque ad 150μ) longis, 30–45μ latis.

Growing on *Codium fragile,* the rhizoidal filaments penetrating deeply into the host, among and beyond the utricles. La Jolla, California. Type, Gardner, no. 3540 (Herb. Univ. Calif., no. 206996), December.

The nearest relative of *E. flocculiformis* apparently is *E. cylindricus* f. *codiophilus.* One marked difference between it and any of the forms of *E. cylindricus* is in the shape and size of the gametangia. This difference, along with others of less importance perhaps, though apparently constant, seems to be sufficient to warrant keeping it separate.

Ectocarpus fructuosus sp. nov.

Plate 45, figures 1–4

Frondibus floccosis, profuse et alterne ramosis, usque ad 2.5 cm. altis, per filamenta copiosa, repentia et comparate brevia affixis; filamentis erectis basi repetite furcatis, ramos longos ramulis ordinum duarum trium*que* brevibus obtusisque ubique circumdantes producentibus; cellulis filamentorum primariorum erectorum cylindricis usque ad leviter doliiformibus et parte ad dissepimenta constrictis, inferne 18–25μ diam., 2–4-plo longioribus quam latis, superne leviter latioribus brevioribusque; zoosporangiis ignotis; gametangiis numerosis, late conicis, sessilibus aut 1–3-cellulato pedicellatis, 50–70μ longis, basi 25–35μ latis.

Growing on the pneumatocyst of *Nereocystis Luetkeana*. Moss Beach, San Mateo County, California. Type, Gardner, no. 4568 (Herb. Univ. Calif., no. 207000), April.

Ectocarpus fructuosus comes within the *E. confervoides* group, but seems amply distinct from any known forms to constitute a species. This species is based upon the character of the branches, viz.; numerous long branches, producing throughout a great abundance of short, rather blunt ramuli, and upon the very numerous, rather short and blunt, predominatingly sessile gametangia. The species seems to be rare.

Ectocarpus granulosoides sp. nov.

Plate 45, figures 7, 8

Frondibus 2–3 cm. altis, profuse ramosis; filamentis primariis subdichotome ramosis, ramis omnibus basi abrupte attenuatis, inferne corticulatis; filamentis secundariis plerumque alternis, partim secundis, strictis, longe attenuatis, acutis, non piliferis, ramulis ultimis plerumque secundis, acutis; cellulis filamentorum primariorum 70–80μ diam., 0.5–1-plo longioribus quam latis, filametorum secundariorum 30–40μ diam., 0.3–1-plo longioribus quam latis, ramulorum ultimorum 14–20μ diam., 0.3–1.5-plo longioribus quam latis, omnibus ad dissepimenta leviter constrictis; chromatophoris numerosis, in cellulis vetustioribus discoideis, in cellulis ramulorum irregulariter angulosis; cellulis filamentorum corticantum 7–10μ diam., 3–4-plo longioribus quam latis; zoosporangiis ignotis; gametangiis in latere superiore ramulorum ultimorum penultimorum*que* secundis, sessilibus, subfusiformibus, asymmetricis, 40–60μ longis, 12–20μ latis.

Growing on rocks(?). San Pedro, California. Type, Setchell, no. 1156*a*, December, 1895.

The very distinct species we have described under the name of *Ectocarpus granulosoides* has the habit of a small *E. granulosus* and

gametangia of the same general type as found in that species, but considerably smaller. The branching, however, is never opposite, and the acute ramuli gradually attenuated upward recall those of *E. acutus*, from which our species is amply distinct in both chromatophore and characters of its gametangia. The branches, particularly the larger, are very suddenly and considerably attenuated at the base, giving the species a striking characteristic of its own, at least within the group of species with discoid chromatophores.

Ectocarpus Mesogloiae sp. nov.

Plate 45, figures 5, 6

Frondibus minutis, 0.75–1.5 mm. altis, per filamenta copiosa, dense intertexta ramosa, rhizoidea, inter callulas hospitis penetrantia affixis; filamentis erectis sparse alterneque ramosis; filamentis primariis et ramulis superne longe attenuatis, acutissimis, non piliferis; cellulis cylindricis, ad dissepimenta leviter constrictis, basi 15–18μ diam., 1–2-plo longioribus quam latis, apicibus filamentorum 4–6μ diam.; chromatophoris tenuibus, irregulariter taeniatis, parietes cellularum fere tegentibus; zoosporangiis ignotis; gametangiis anguste cylindrico-conicis, 120–160μ (usque ad 210μ) longis, 18–22μ latis, brevi-pedicellatis, raro sessilibus.

Growing on *Mesogloia Andersonii*. Carmel Bay, Monterey County, California. Type, Gardner, no. 2865*a* (Herb. Univ. Calif., no. 206989), May, 1915.

The general characters of this diminutive species ally it with the *E. confervoides* group. We have deemed it best to consider it a distinct species on account of the small dimensions of all of its parts and its penetrating habit. It has not been seen on any other host except the one mentioned above.

Ectocarpus Saundersii sp. nov.

Frondibus floccos parvos 2–5 mm. altos formantibus, per filamenta copiosa, ramosa, in superficiem hospitis repentia affixis; ramis alternis; ramis primariis longis divergentibusque ramulis ultimis sparsis, brevibus, acuminatis; cellulis filamentorum primariorum 25–40μ diam., inferne quadratis, superne brevioribus, ad dissepimenta leviter constrictis; chromatophoris numerosis, discoideis; zoosporangiis breviter pedicellatis aut intercalaribus, globosis, ad 30μ diam.; gametangiis cylindricis usque ad ovoideis, obtusis aut acuminatis, lateralibus, pedicellis longioribus aut brevioribus suffultis, 70–150μ longis, 25–50μ latis.

Growing on *Fucus*, in the middle of the littoral belt. Pacific Grove, California.

Ectocarpus paradoxus var. *pacificus* Saunders, Phyc. Mem., 1898, p. 152, pl. 18, figs. 4–7; Collins, Holden, and Setchell, Phyc. Bor.-Amer. (Exsicc.), no. 530.

According to Saunders, his plant, the var. *pacificus*, differs from the type of *E. paradoxus* Mont., in lacking any manifestation of opposite branching as well as in having the gametangia longer and more pointed. In these respects and also in that it is a shorter plant, it seems to us to be sufficiently distinct to be separated specifically from the type, and to be different from any other species known to us. We are consequently dedicating it to its discoverer.

Ectocarpus simulans sp. nov.

Plate 45, figures 9–11

Frondibus 1–2 mm. altis, floccosis; filamentis prostratis tortuosis, discretis; filamentis erectis simplicibus, superne leviter attenuatis, non piliferis; cellulis cylindricis, ad dissepimenta non constrictis, medio 11–13μ diam., 1–2.5-plo longioribus quam latis; chromatophoris taeniatis, parietes cellularum prope exacte tegentibus, paucis; zoosporangiis ignotis; gametangiis lateralibus aut interdum terminalibus, sessilibus, anguste ellipsoideis, obtusis, plerumque leviter curvatis, 55–65μ longis, 15–20μ latis.

Growing on *Chaetomorpha aerea*. Cypress Point, Monterey County, California. Type, Gardner, no. 3087 (Herb. Univ. Calif., no. 206993), December.

The present species resembles, in general, certain forms of *Ectocarpus pusillus* Griffiths (cf. Sauvageau, 1895), but the erect filaments are much more slender, usually never branched, and with much smaller gametangia. It forms tufts on *Chaetomorpha aerea*, whose filaments are encircled by the prostrate filaments of the *Ectocarpus* which form small cushions in their growth over one another. The gametangia are rather blunt and often more or less curved.

Ectocarpus socialis sp. nov.

Plate 46, figures 12, 13

Frondibus caespitosis, 1–3 mm. altis, per filamenta rhizoidea dense intricata et penetrantia affixis; filamentis erectis, ad superficiem hospitis, repetite furcatis, superne simplicibus aut alternate-ramosis, longe attenuatis et piliferis; cellulis cylindricis usque ad leviter dolii-

formibus, non constrictis, 22–28μ diam., inferne 1–2-plo, superne 1–2-plo longioribus quam latis; chromatophoris parvis, in cellula quaque paucis, discoideis; zoosporangiis ellipsoideis, erectis, lateralibus, alternis 1–2-cellulato-pedicellatis, interdum prope basim filamentorum erectorum sessilibus, 60–95μ longis, 35–50μ latis; gametangiis fusiformibus, sparsis, partes superiores filamentorum erectorum occupantibus, sessilibus aut 1–2-cellulato-pedicellatis, alternis 70–85μ longis, 25–30μ latis.

Growing on *Codium fragile* (Suringar) Hariot, in company with *Ectocarpus globifer* Kuetz. and with various species of Myxophyceae and Rhodophyceae. Redondo, California. Type, Gardner, no. 1947*b* (Herb. Univ. Calif., no. 206987), March.

Ectocarpus socialis seems to be a relative of the *E. cylindricus* group. The chief distinctions are in the shape, size, and position of the gametangia.

Ectocarpus Taoniae sp. nov.

Plate 46, figure 15

Frondibus diffusis, 0.5–1.5 mm. altis, per filamenta superficialia repentia, profuse ramosa affixis; filamentis erectis simplicibus, basim leviter attenuatis, superne longe attenuatis, piliferis; cellulis, filamentorum repentium cylindricis, 4–6μ diam., filamentorum erectorum 8–10μ diam., inferne quadratis, apicibus 4–6-plo longioribus quam latis; chromatophoris curtis, comparate crassis, irregulariter taeniatis; zoosporangiis ignotis; gametangiis anguste ellipsoideis, interdum lente curvatis, in filamentis repentibus et erectis plerumque sessilibus, 20–28μ (usque ad 40μ) longis, 15–20μ latis.

Growing on *Taonia Lennebackerae*. San Pedro, California. Type, Gardner, no. 3561*a* (Herb. Univ. Calif., no. 206997), December.

This species forms rather diffuse and even layers, mostly along the margins of *Taonia*, over whose surface the creeping filaments spread and give rise to gametangia or to erect filaments not over 1.5 mm. high. In many ways it seems like a miniature *Ectocarpus Padinae* (Buffh.) Sauvageau (1897, p. 30 *et seq.*). Our species, however, is only about half as tall, the cells of the erect filaments about half as broad, and the gametangia less than half as large as those of *E. Padinae*. We have found gametangia only of the "antheridium" type. *Ectocarpus Padinae* has its creeping filaments entirely endophytic while *E. Taoniae* has them entirely epiphytic.

Ectocarpus confervoides f. **parvus** (Saunders) comb. nov.

Fronds gregarious, forming tufted or extended masses, 1–2 cm. high, more or less alternately branched; erect filaments 21–30μ broad, slightly constricted at the joints, much attenuated at the tips or ending in hairs; cells 1–3 times as long as broad below, shorter above; chromatophores irregularly band-shaped; zoosporangia ovoid or ellipsoid, 35–55μ long, 20–27μ broad, usually sessile, sometimes on the same filament with the gametangia; gametangia narrowly lanceolate-conical, gradually long attenuated above, 120–400μ long, 20–27μ broad, borne on a longer or shorter pedicel, occasionally seriate and intercalary (as in *Pylaiella*).

On sand-covered rocks (type!), logs, or on the larger Melanophyceae. Central California (near San Francisco) and southern California (San Pedro, the type locality, and San Diego).

Ectocarpus siliculosus parvus Saunders, Phyc. Mem., 1898, p. 153, pl. 22, figs. 1–9.

The f. *parvus*, as defined above, presents certain resemblances to both *Ectocarpus siliculosus* and *E. confervoides*. Its slender elongated gametangia resemble those of *E. siliculosus* and much might be said in favor of the opinion of Saunders in making it a "variety" of that species. On the other hand, very few, or none, of the typical gametangia end in a hair and we have therefore preferred to place it rather with *E. confervoides*. There are often found in this form, as well as in forms of *E. siliculosis*, very curious, elongated, intercalary gametangia which seem to be seriate in that they open laterally in sections, as do those of *Pylaiella*. Such gametangia are very puzzling, but may possibly be regarded as indicating hybridization between *Pylaiella* and *Ectocarpus* or a mutation of some sort. Speculation, however, can scarcely explain such anomalies. The majority of the gametangia are typically of *Ectocarpus* and while approaching in shape those of *E. siliculosus*, are less slender and less elongated than is typical for that species and are not ordinarily prolonged into terminal hairs.

So far as we may judge from the scanty specimen in our copy, no. 358 of Tilden's American Algae (from Pacific Grove) belongs rather under f. *parvus* than f. *variabilis*, although the determination as f. *variabilis* is attributed to Saunders.

Ectocarpus cylindricus f. **typicus** nom. nov.

Fronds diffused, 1–2 mm. high; creeping filaments superficial; erect filaments very sparingly branched above, several arising from the same creeping filament, tapering slightly at the base and apex; cells of the creeping filaments 16–20μ diam.; cells of erect filaments cylindrical, slightly constricted at the cross-walls, 2–3 times as long as broad below and at the apex, 0.5–1 times in the middle of the filament; gametangia mostly on the middle and upper parts of the filaments, mostly alternate.

Growing on *Egregia Menziesii, Halidrys dioica* and *Cystoseira osmundacea*. The type locality is Pacific Grove, California.

Ectocarpus cylindricus f. **codiophilus** f. nov.

Plate 46, figure 14, and Plate 49, figures 42–45

Frondibus dense caespitosis, 3–5 mm. altis, per filamenta rhizoidea dense intricata, hospitem penetrantibus; filamentis erectis prope superficiem anastomosantibus et furcatis, superne eramosis, piliferis, gametangiis plerumque prope basim filamentorum erectorum sitis.

Growing on *Codium fragile* (Suringar) Hariot and *Codium Setchellii* Gardner. Carmel Bay, Monterey County, California, and La Jolla, San Diego County, California. Type, Gardner, no. 3540*a* (Herb. Univ. Calif., no. 206992), December.

This form differs from f. *typicus* in having penetrating rhizoidal filaments and in that the gametangia are gathered in a dense zone at or near the base of the erect filaments instead of being scattered.

Ectocarpus cylindricus f. **acmaeophilus** f. nov.

Plate 49, figure 46

Frondibus floccosis, 7–10 mm. altis; filamentis repentibus superficialibus, filamentis erectis eramosis, diametro in parte quaque similibus; zoosporangiis ignotis; gametangiis usque ad 270μ longis, plerumque in parte superiore filamentorum erectorum oppositis.

Growing on *Acmaea* sp. Carmel Bay, Monterey County, California. Type, Gardner, no. 2884 (Herb. Univ. Calif., no. 206990), May.

This form seems to be rare, at least but few specimens have been detected up to the present time. It differs from f. *typicus* in being practically unbranched, except the fructiferous branches. Where branches occur, they seem to arise as the result of an injury to the main filament. It differs further in that the erect filaments are more nearly cylindrical throughout, and the gametangia more often opposite and generally longer and proportionally narrower.

Ectocarpus siliculosus f. **subulatus** (Kuetz.) comb. nov.

Fronds 5–25 cm. high, light yellow, fleecy, much branched, not constricted at the joints; branches long, attenuated above, many ending in a long hair; cells of the main filaments 30–36μ broad, 1–1.25 times as long as broad, zoosporangia unknown; gametangia elongated subulate-ovoid, some stouter, some more slender, 200–600μ long, 12–48μ broad, the upper (and as a rule more slender) usually terminating in a hair, on a 2–10 or 12 celled pedicel.

In brackish pools, on sticks or grasses. Central California (San Francisco Bay).

Ectocarpus confervoides f. *subulatus* Collins, Holden, and Setchell, Phyc. Bor.-Amer. (Exsicc.), no. 1231. *Ectocarpus subulatus* Kuetzing, Spec. Alg., 1849, p. 454. Tab. Phyc., vol. 5, 1885, p. 19, pl. 61, fig. II. *Ectocarpus confervoides* Hauck, Meeresalg., 1884, p. 331 (excl. synonomy). *Ectocarpus amphibius* Harvey, Phyc. Brit., vol. 2, 1848, pl. 183, Ner. Bor.-Amer., part III, 1858, p. 125.

Our plant seems to agree very well with the figures and description of *Ectocarpus amphibius* Harvey and also, although not so perfectly, with *E. subulatus* Kuetz. They are both brackish water forms, as are our plants. Hauck refers to his var. *subulatus* also *Ectocarpus draparnaldiaeformis* Kuetz. and *E. macroceras* Kuetz. Judging from Kuetzing's illustrations, these two species may be forms of *E. siliculosus* but are not to be included under f. *subulatus*.

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PLATE 45

Ectocarpus fructuosus S. and G.

Fig. 1. Diagrammatic illustration of whole plant.

Fig. 2. Part of a plant showing positions and various shapes and sizes of the gametangia. × 175.

Figs. 3, 4. Terminal ramuli showing variations in shape of cells and somewhat reduced gametangia. × 60.

Ectocarpus Mesogloiae S. and G.

Fig. 5. A single gametangium and a piece of terminal ramulus illustrating chromatophores and cells. × 200.

Fig. 6. A group of plants showing rhizoids, character of branching, relative shapes and sizes of gametangia. × 40.

Ectocarpus granulosoides S. and G.

Fig. 7. A group of terminal ramuli showing character of branching, shapes of cells, positions and shapes of gametangia. × 125.

Fig. 8. A few cells of the main filament showing the shapes of cells and of chromatophores. × 125.

Ectocarpus simulans S. and G.

Fig. 9. Diagrammatic illustration of groups of plants on their host.

Fig. 10. Parts of plants showing shapes and positions of gametangia. × 125.

Fig. 11. A group of cells of the main filament showing chromatophores. × 250.

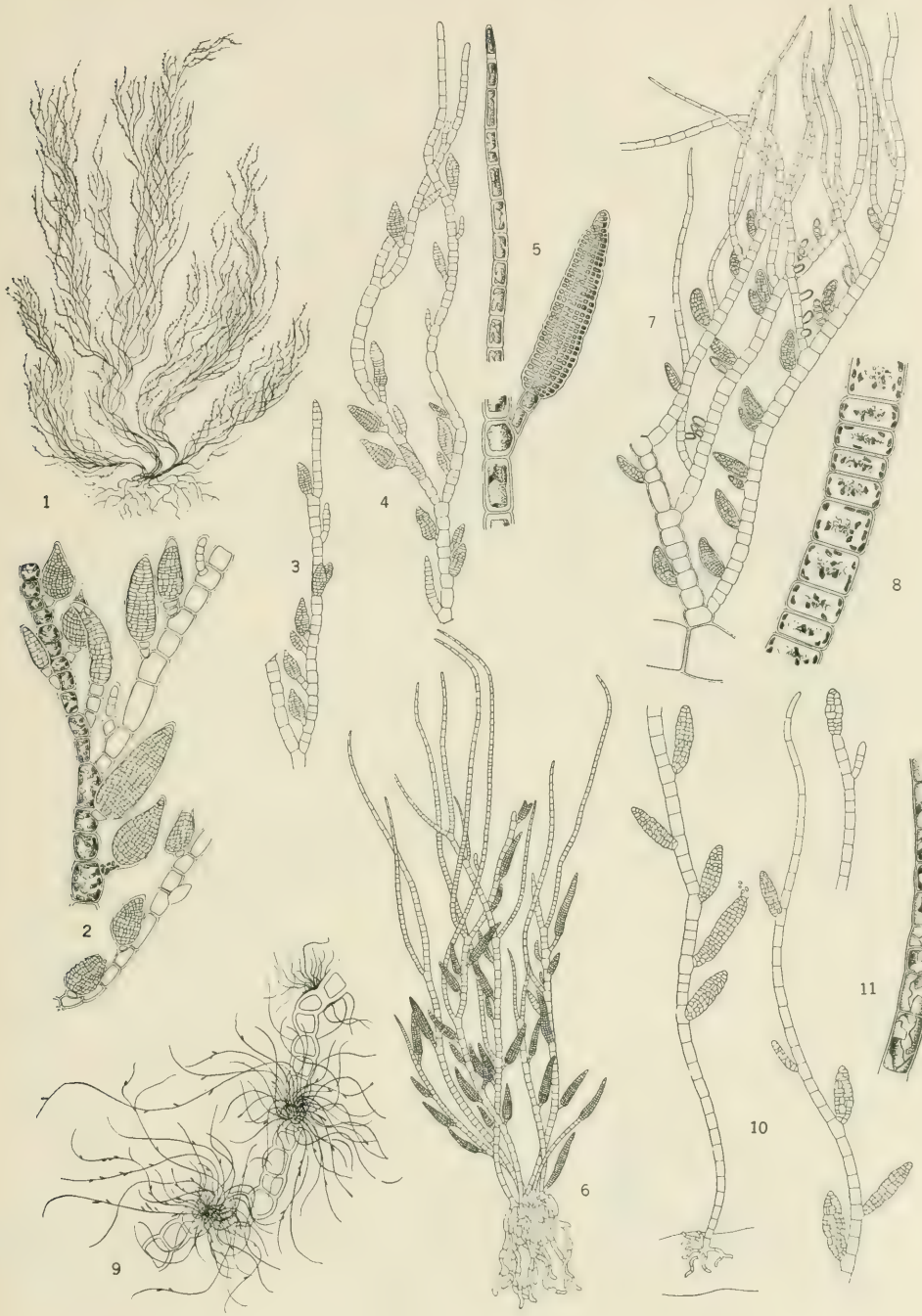
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PLATE 46

Ectocarpus socialis S. and G.

Fig. 12. A small group of plants showing rhizoids, a few cells with chromatophores, and the positions and shapes of the zoosporangia. × 125.

Fig. 13. A selection of parts of filaments showing the positions and relative shapes and sizes of the gametangia. × 125.

Ectocarpus cylindricus f. *codiophilus* S. and G.

Fig. 14. A group of young plants showing both zoosporangia and gametangia, the two parts of ramuli on the left representing these organs on the same plant. × 60.

Ectocarpus Taoniae S. and G.

Fig. 15. A portion of a creeping filament showing erect filaments and the positions and relative shapes and sizes of the gametangia on both the creeping and the erect filaments. × 250.

Ectocarpus affinis S. and G.

Fig. 16. Diagrammatic representation of a small group of plants on their host.

Fig. 17. Portions of filaments illustrating positions, relative shapes and sizes of gametangia. × 225.

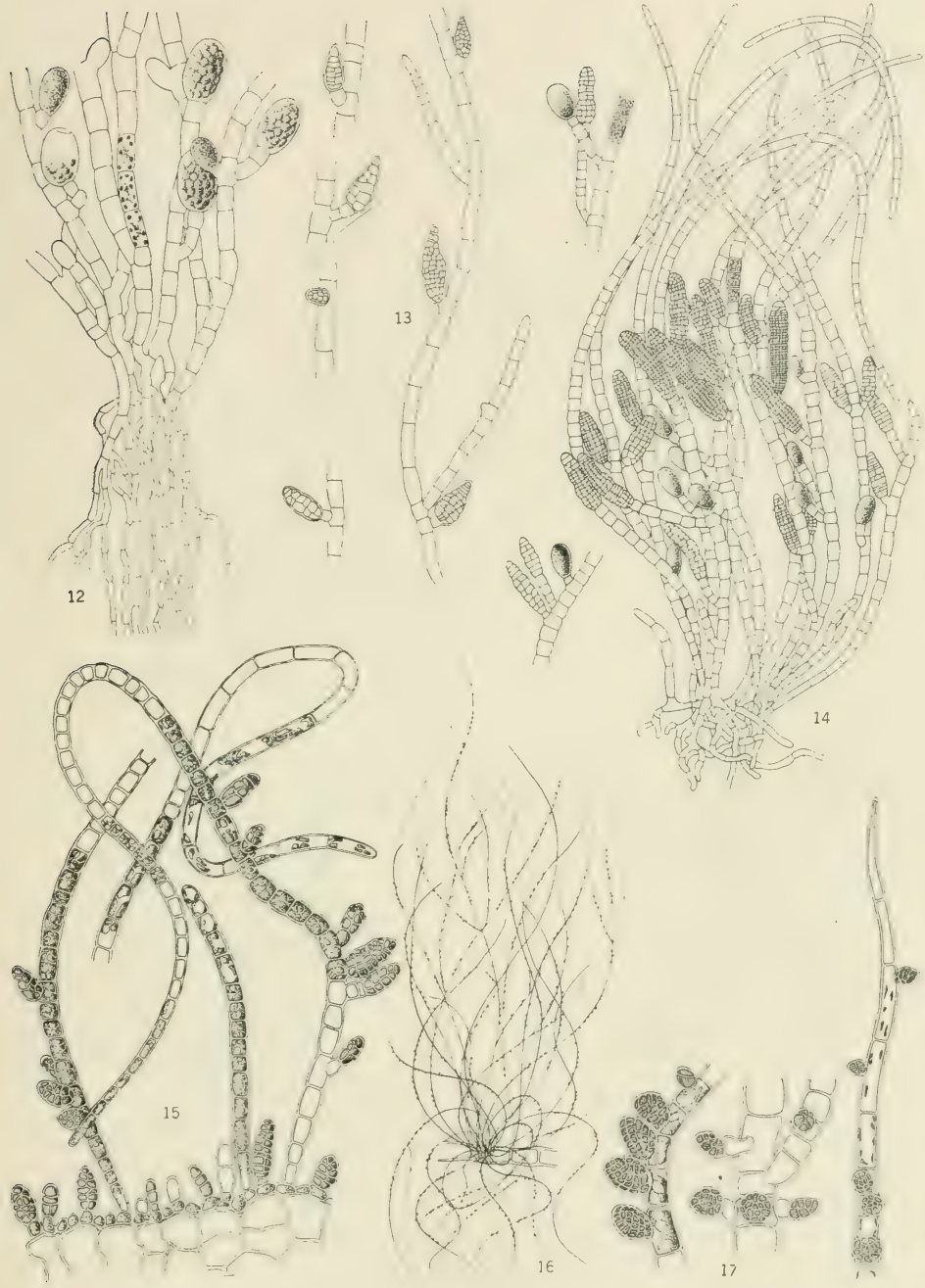
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PLATE 47

Ectocarpus eramosus S. and G.

Fig. 18. A group of typical gametangia showing the range of relative shapes and sizes. × 60.

Fig. 19. Part of a filament showing an intercalary gametangium. × 60.

Fig. 20. A part of a filament near its outer end, showing variation in shapes and sizes of the cells and scattered dwarf gametangia. × 60.

Fig. 21. The basal parts of a group of erect filaments showing long rhizoidal filaments. × 60.

Fig. 22. A filament showing two gametangia with long pedicels. × 60.

Fig. 23. Terminal parts of filaments, one showing chromatophores. × 60.

Ectocarpus flocculiformis S. and G.

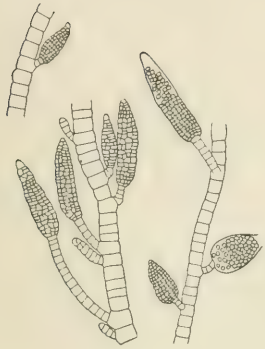
Fig. 24. A group of filaments anastomosing at the base and developing numerous rhizoids and characteristic gametangia. × 125.

Ectocarpus flagelliferus S. and G.

Fig. 25. Showing an intercalary gametangium. × 125.

Fig. 26. Showing normal gametangia and chromatophores. × 125.

Fig. 27. Showing basal parts of filaments. × 125.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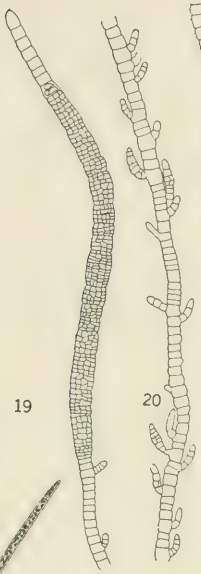
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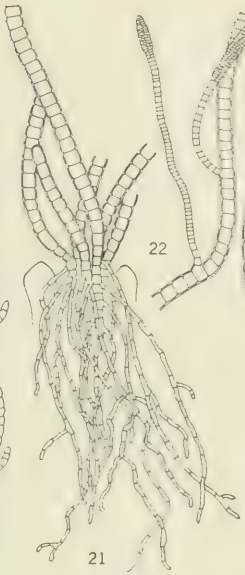
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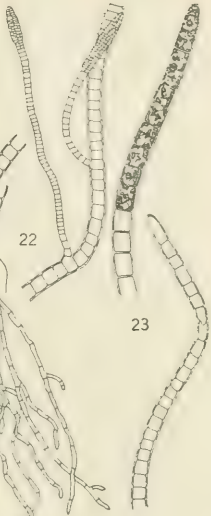
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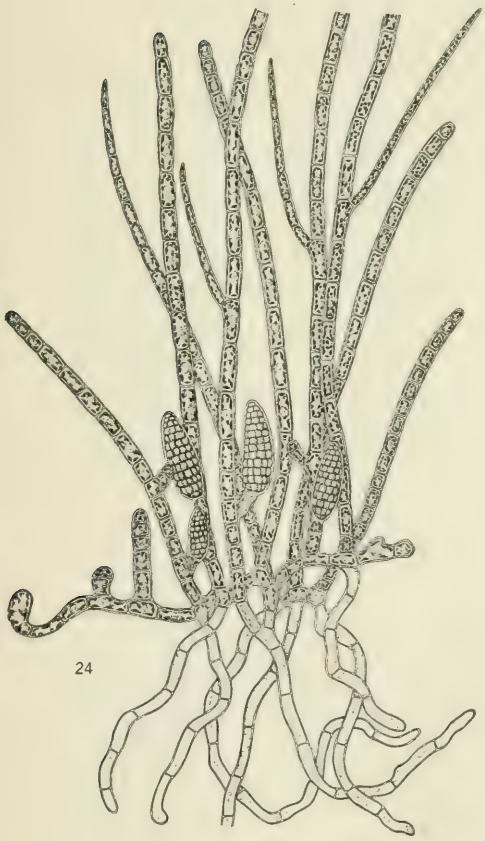
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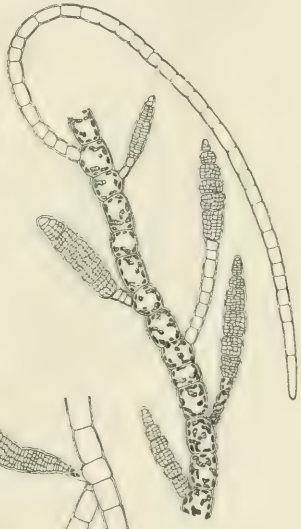
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PLATE 48

Ectocarpus chantransioides S. and G.

Figs. 28, 29. Characteristic terminal ramuli with characteristic gametangia. × 150.

Fig. 30. Diagrams showing the pulvinate habit of growth. One in the upper right-hand corner represents a vertical section view.

Fig. 31. Illustrating the creeping filaments. × 150.

Ectocarpus commensalis S. and G.

Fig. 32. A group of plants with relatively long gametangia. × 50.

Fig. 33. A single typical gametangium and parts of filaments showing chromatophores. × 225.

Fig. 34. A group of young filaments with long rhizoids.

Fig. 35. A group of plants showing their relation to the host. Diagrammatic.

Ectocarpus acutus S. and G.

Fig. 36. A diagrammatic illustration showing method of branching and the shape and position of the gametangia.

Fig. 37. A group of gametangia showing some variations in form and size. × 125.

Fig. 38. A piece of a filament showing shapes of cells and chromatophores. × 125.

Fig. 39. A few terminal acute ramuli. × 125.

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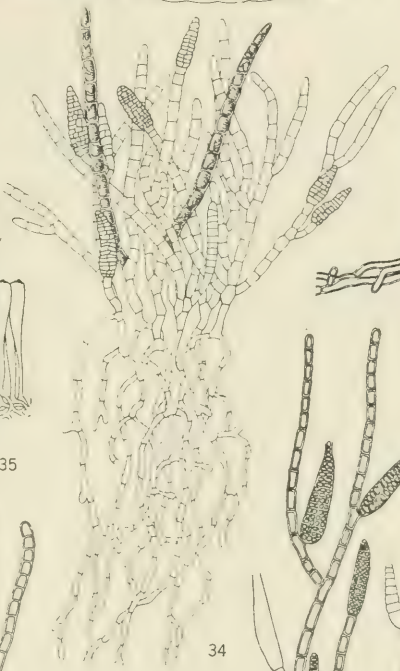
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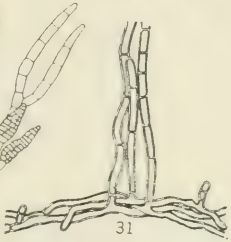
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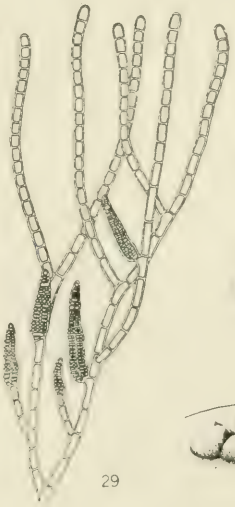
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PLATE 49

Ectocarpus acutus S. and G.

Fig. 40. A group of terminal ramuli bearing numerous complex zoosporangia(?). × 125.

Fig. 41. A group of typical gametangia. × 125.

Ectocarpus cylindricus f. *codiophilus* S. and G.

Fig. 42. Piece of a filament bearing zoosporangia. × 125.

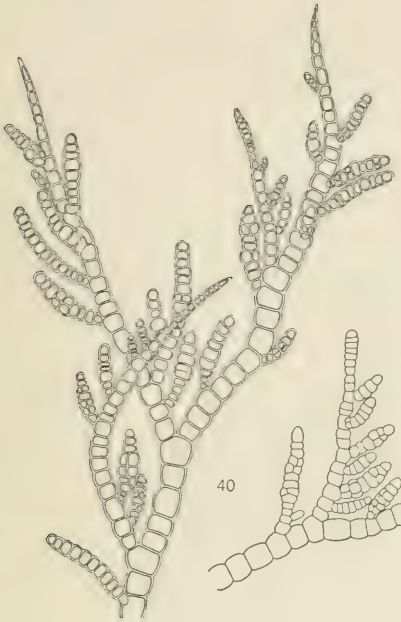
Fig. 43. Piece of a filament bearing opposite typical gametangia. × 125.

Fig. 44. Piece of a terminal filament bearing zoosporangia. × 125.

Fig. 45. A group of plants showing the typical crowded basal gametangia. × 65.

Ectocarpus cylindricus f. *acmaeophilus* S. and G.

Fig. 46. Piece of a typical filament bearing opposite sessile gametangia. × 65.



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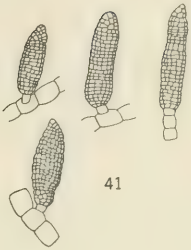

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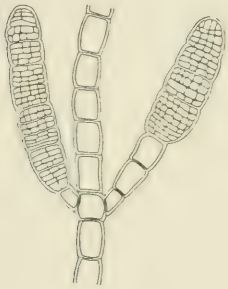

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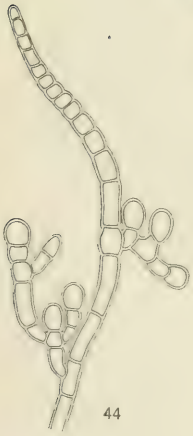

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NOTES ON PACIFIC COAST ALGAE

II. ON THE CALIFORNIAN "DELESSERIA QUERCIFOLIA"

BY
CARL SKOTTSBERG

During my visit to California in 1913 Professor W. A. Setchell introduced me to a red alga called *Delesseria* (or *Schizoneura*) *quercifolia* by American algologists and identified by them with a plant described by Bory in Voyage sur "La Coquille," Cryptogamie, p. 136, table 18, fig. 1, from the shores of subantarctic America. However, it appeared to me that it was different from this latter, which I had collected at various occasions on the coasts of Tierra del Fuego and the Falkland Islands, where it is one of the commoner species. When preparing the paper on my collection of 1902 I compared my material of Bory's species with a specimen from California in Herb. Stockholm, and stated that the latter belongs to a different yet undescribed species (see Kylin and Skottsberg, "Zur Kenntnis der subantarktischen und antarktischen Meeresalgen II," p. 94, Wiss. Ergebn. der schwed. Südpolar-Exp., IV:15, 1919).

In order to make a more careful comparison between the two species, I asked Professor Setchell for some material from California, and he most willingly sent me a good set of specimens with all kinds of reproductive bodies, for which I give him my best thanks. As all the material is dry, it has not been possible to enter into histological details regarding the formation of spermatia, cystocarps, or tetraspores, but this does not, I dare say, prevent us from arriving at a safe conclusion as to the systematic position.

Both species agree in most characters and are nearly related to each other, but well separated from other species. In both the frond consists of an oblong, short, stipitate lamina of ordinary size, with more or less sinuate margins, monostromatic except for the costa and nerves; as usual, the parts where tetraspores, etc., are formed

become polystromatic. The costa is very conspicuous and of the same anatomical structure in both, it emits opposite, nearly straight to irregularly bent, distinct nerves. The ramification from the lamina is marginal, solitary segments growing out to form new blades. When the lamina has worn away numerous shortly stipitate proliferations grow out from the edges of the old, flattened costa. The hapter is a small disc.

The cystocarps are scattered between the nerves, and the same position is occupied by the spermatangia and tetrasporic sori, the latter often occupying the entire space between the costa and the margin of the frond, only leaving the nerves free. Further, both species have exactly the same mode of apical growth (see below).

The Californian plant differs from the true *D. quercifolia* in the following characters: The frond is more oblong, lingulate, and, except for the segments growing out to form branches, entire, or only slightly undulate and denticulate. The frond of *D. quercifolia* Bory is more broadly obovate in outline, more or less deeply sinuate-dentate, young intact specimens recalling the leaves of the common European *Quercus robur* and very similar to *D. sinuosa* of the northern coasts. The anatomical structure is the same in all these species. To judge from the material examined there is some little difference in the costa between the Californian species and *D. quercifolia*. In the former (fig. 1) the central lamella consists of one layer of very large cells, corresponding to the monostromatic lamina; and even the innermost cortical cells are much smaller, each cell, on the cross-section, supporting one or two rows of radially arranged cells. In *D. quercifolia* there generally are as much as five layers of large cells, because the inner cortical strata are more similar to the central lamella and contrasting with the outer radial rows of small cells, but in other cases this structure has proved to be submitted to some variation, so we should not lay very great weight upon this difference.

Anyhow we have to do with two distinct species belonging to the same genus. *D. quercifolia* Bory is sometimes called *Schizoneura quercifolia* (Bory) J. Ag. and, if we follow Agardh, it lies near at hand to describe the other as a new species of *Schizoneura*. But if we advance deeper into this matter we shall find that Agardh's genus is a *mixtum compositum*, and that we cannot arrive at a solution unless entering upon the history of the genus *Delesseria* and the systematic value of some of the genera created by Agardh in Sp. Alg. III:3 (1898).

Ruprecht gave a summary of the history of nomenclature in "Tange des Ochotsch. Meeres," p. 250. When Lamouroux established the genus *Delesseria* there was an older name for it, *Hydrolapatha* (*-um*) Stackhouse, pp. 54, 67, Tont. marino-crypt. II (1809). Stackhouse listed six species, among them *H. sanguinea* and *H. sinuosa*. But the name *Delesseria* continued to be generally used, and this caused the Brussels Congress, 1910, to put it on the list of "genera conservanda" and to reject *Hydrolapatha* in spite of being older. I think we had better agree to this proposal. *D. sanguinea*, mentioned first under *Delesseria* by Lamouroux, should be regarded as the type of the genus.

In Phycol. Gener. (1843) Kützing had established two new genera, *Phycodrys*, based on *D. sinuosa*, and *Hypoglossum*, with *H. Woodwardii* (*D. hypoglossum*) as type. In Sp. Alg. (1849) the same subdivision is retained. Here we need not occupy ourselves further with Kützing's system. Schmitz (Rhodophyceae in Engler and Prantl's Natürl. Pflanzenfam.) rejected both *Phycodrys* and *Hypoglossum*, but at the same time expressed the view that the genus *Delesseria* ought to become split up, though the time when this might be done in a proper manner had not yet arrived.

In Sp. Alg. III:1 (Epicrisis systematis floridearum, 1876) J. G. Agardh divided *Delesseria* into thirteen sections: *Schizoneura* was one of these, characterized by the lamina being "subvage laciniato-partita" and by the tetraspores situated on the main frond between the nerves. Sect. *Phycodrys* had "frondes sinuato-pinnatifidae" and sori along the costa or in the tips of the segments, or in separate leaflets. *D. sanguinea*, the typical species of the genus, was excluded from the order and brought to the Rhodymeniaceae as a monotypic genus *Hydrolapathum*. During the whole of his life Agardh firmly adhered to this peculiar idea. In the monograph on the Delesseriaceae, Sp. Alg. III:3 (1898), the sections of 1876 were given generic rank. The genus *Schizoneura* is now characterized mainly by the formation of tetrasporangia: the sori are called "gemini" and "oppositi," while they are called "singuli" in other genera, where two sporangia, according to Agardh, were not formed opposite to each other on the two pages of the frond. This was the case, f. i., in *Delesseria* in Agardh's sense: this name is applied to his former section *Phycodrys*. I cannot see this point of difference, as sections through the sporophylls of *D. sinuosa* show a bilateral development of the sori just as in *Schizoneura quercifolia*. Further, the anatomical structure and mode of growth

are identical in both. But *Schizoneura* comprises several species. *S. subcostata*, J. Ag., is mentioned first and should, perhaps, be regarded as the type; in any case, *quercifolia* was declared by Agardh to be a non-typical member of the genus. I have examined part of the original material of *S. subcostata*, coll. by Schousboe. Here the costa does not reach to the top of the frond, the top-cell soon loses its leading position and can hardly be traced in the older lamina, stray marginal cells become centers of action, soon replaced by others; we find conditions characteristic of *Nitophyllum*, and the anatomical structure, with little or no difference between the central lamella and the cortex, is quite nitophylloid. This may also be seen from Agardh's illustrations on plate 26 in "Florideernes morfologi" (K. Sv. Vetensk. Akad. Handl. 15:6, 1879); the figure of a growing apex is rather idealized. Of *S. Davisii* (Hook. fil. et Harv.) J. Ag., I have examined Hooker's type (Herb. Kew). This is still more like a *Nitophyllum*, as even in very small proliferations no active top-cell is present, the growth being marginal and intercalary. But in *S. quercifolia* the costa can be followed right through to a typical, active top-cell, just as in *D. sinuosa*. The nerves in *S. subcostata, Davisii*, etc., are not opposite, but generally very irregular. There are hardly any nerves exactly corresponding to the regular opposite ones in *S. quercifolia*, which must be excluded from Agardh's genus.

In the "Nachtrag" to Schmitz' Rhodophyceae, by N. Svedelius (1911), some of Agardh's new genera were recognized and others, among them *Schizoneura*, rejected. So if we follow Schmitz and Svedelius, *Delesseria* comprises *sanguinea*, *sinuosa*, *quercifolia*, *hypoglossum*, etc. Of course neither of those authors was satisfied with this arrangement; only, as Svedelius expresses himself, as long as our knowledge of the various types is so insufficient as it is now, it seems better to regard some of Agardh's genera as divisions of *Delesseria*. Still, I think that Nienburg's studies, also quoted by Svedelius, permit us to reëstablish Kützing's genus *Phycodrys*, with *Ph. sinuosa* as type.

The mode of growth in the apex of the Delesseriaceae has been studied by various authors, including Nägeli, Wille, Oltmanns. Lately Nienburg made a critical examination of numerous species and published his results under the title "Zur Keimungs-und Wachstumsgeschichte der Delesseriaceen" (Bot. Zeitung, 66, 1908). Of species of *Delesseria* (taken in its widest sense) he examined *sanguinea*, *sinuosa*, *Lyallii*, *alata*, and *hypoglossum*. He distinguishes

two types of apical growth, the *hypoglossum*-type and the *sinuosa*-type. The difference between them, as described and illustrated by Nienburg, may be summarized as follows. Both have a central axis with a primary top-cell and regular opposite branches, each ending in a secondary top-cell. In the *hypoglossum*-type these branches of 1. order carry, on their external side, branches of 2. order, each ending in a tertiary top-cell (fig. 2). In the *sinuosa*-type such top-cells do not become developed: the cells of the branches of 1. order are divided by length and cross-walls, but we do not find the regular arrangement of branches second order as in the other type. Thus the appearance of the growing apex becomes quite different in the two cases. To the *hypoglossum*-type also belong *D. sanguinea* and *alata*, to the *sinuosa*-type, *D. Lyallii*.

It was easy to see that *D. quercifolia* Bory as well as the Californian species belong to the *sinuosa*-type. But when it came to the analysis of the mode of development I could not bring my results in accordance with Nienburg's scheme. Anybody comparing my figure 3 with his figures 16 and 44 will discover the difference. And as the plasma connections designed by the writer were observed on alcohol material, while Nienburg's analytical scheme is a construction, I concluded that the latter was not correct, or that, after all, *D. quercifolia* differed from the *sinuosa*-type. I had a discussion on this matter with Professor H. Kylin, who has occupied himself with an examination of *D. sinuosa*. He kindly informed me that Nienburg's explanation of the growth is partly incorrect and that, in fact, the development is the same in *sinuosa* and *quercifolia*. Nienburg's types will stand, their systematic importance will prove to be very great, but the main point of difference seems to have escaped his full attention. In the *hypoglossum*-type, the cells of the main axis keep pace with the development of the branches of 1. and 2. orders by getting elongated, while, in the *sinuosa*-type, they become divided by intercalary cross-walls (a well-known fact), and the intercalary cells thus formed develop short, few-celled branches which become inserted between the branches of 1. order. This system of intercalary branchlets is dotted in figure 3. The same mode of growth is repeated in the branches of 1. order. Thus it is easy to understand why the beautiful cellular architecture of a *D. hypoglossum* is lost in *D. sinuosa* or *quercifolia*. In the Californian species, owing to the dry material, no plasma connections were distinctly visible, but a comparison between figures 3 and 4 will show that the development is the same in both cases.

I have examined a great number of species belonging to the present tribe Delesseriae as to the mode of growth, anatomical structure, position of cystocarps and sori, and I believe that I can refer every species to one of the two principal types. There are of course many I have not seen or of which the material was less satisfactory. In all the species of *sinuosa*-growth the cells of the main axis, as told above, get divided by cross-walls, so that the central lamella of the costa is formed by comparatively short cells. A cortex is formed by tangential and radial divisions, the cells being arranged in a regular manner (fig. 1) recalling the cortex in *Nitophyllum*, though the difference between a "medulla" and a "cortex" is more evident than in the latter genus. In the *hypolossum*-type, the costal cell-rows are formed by very long cells: these cut off cortical cells, that divide by radial walls, the cells thus formed get stretched in longitudinal direction, are again divided by a tangential wall, and so forth, so that we observe, on a length section, very long tubes in the center and gradually shorter cells toward the surface. Even in a cross-section of a young costa the radial arrangement is much less distinct than in the other type, and later the difference becomes more marked. The long tubes make the costa a rather weak structure, which is strengthened by the development of numerous narrow hyphae (fig. 5). I have not found such hyphae in any species belonging to the *sinuosa*-type. Those different kinds of anatomical structure have been described and figured before (see Wille, "Beiträge zur Entwickelungsgeschichte der physiologischen Gewebesysteme bei einigen Florideen"—Nova Acta der K. Leop.-Carol. Akad. LII [1887]), but they were not, as far as I am aware, combined with the different modes of apical growth. It should be mentioned that, among species belonging to the *hypoglossum*-type, I have found two with non-typical anatomy, *D. Montagneana* J. Ag. and *D. ruscifolia* Ag., both referred to the genus *Apoglossum* by J. G. Agardh. In these small species hardly any pyphae at all get developed, the differences between "medulla" and "cortex" are marked, but the radial arrangement of cells less distinct than in *sinuosa*, etc. I may add that the larger species, *A. decipiens* J. Ag., has typical *hypoglossum*-structure in the costa. In spite of these apparent exceptions, the anatomical distinction between the two types is obvious.

If *Delesseria sanguinea* be recognized as the type of the genus, *D. sinuosa* must of course be excluded and *Phycodrys* of Kützing be restored. We have seen that *Schizoneura quercifolia* differs from other members of this dubious genus while it agrees with *Phycodrys sinuosa*

(Good. et Wood.) Kütz. in essential characters. The principal difference lies in the position of the tetraspores. In the latter these generally are developed in minute marginal leaflets forming a fringe to the old frond, but they sometimes occur along the margins of the main frond (see Kützing, Sp. Alg., p. 874). I do not think that we can attribute any great importance to this difference, which, in this case, seems to be of a more biological nature. The cystocarps have the same position in both. *Schizoneura quercifolia* will receive the name *Phycodrys quercifolia* (Bory) Skottsb., and the Californian species is distinguished as

Phycodrys Setchellii, nov. spec.

Syn. *Delesseria quercifolia* auctt. quoad plantam californicam, non Bory.

Frons primo simplex, oblonga, lingulata, brevissime stipitata, integra sed margine plus minusve sinuata et denticulata, mox ramificatione marginali parce et irregulariter laciniata, eximie costata et opposite venosa, serius e costa denudata stipitem elongatum formante prolifera. Crescentia apicalis nec non structura anatomica pro genere typica. Spermatangia et tetrasporangia soros inter venas formantia, cystocarpia eodem loco adspersa. Color in sicco sat obscure ruber.—Exs.: Algae exsicc. Amer. Bor. num. 65.—Hab. ad oras Californiae, cum cystocarpiis et spermatangiis in eum tetrasporangia in lecta.

The largest specimen at hand measures about 15 cm.; simple fronds and marginal proliferations are up to 10 cm. long and 3 cm. broad, with their greatest width generally a little above the middle. In old specimens, the lower part of the primary costa forms a conspicuous stipe, and the older proliferations are distinctly pedicellate.

Botanic Garden, Gothenburg, Sweden,
October, 1921.

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EXPLANATION OF PLATE 50

Fig. 1. Cross-section through the costa of *Phycodrys Setchellii.*

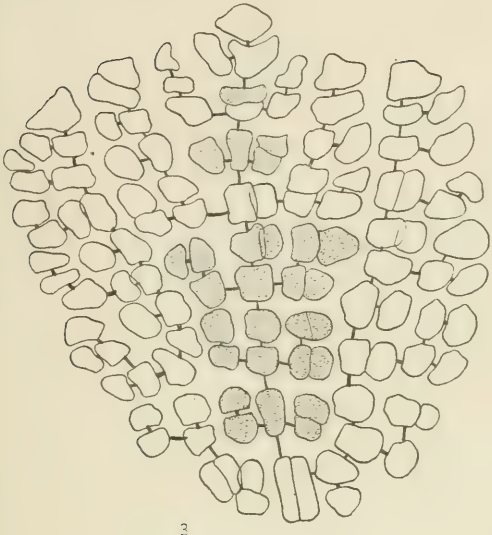
Fig. 2. Growing apex of *Hypoglossum Wodwardii.*

Fig. 3. Growing apex of *Phycodrys quercifolia.* Intercalary cells and branchlets of the main axis dotted.

Fig. 4. Growing apex of *Phycodrys Setchellii.* In the lower part the formation of cortical cells has begun.

Fig. 5. Cross-section through the stipe of *Hypoglossum Woodwardii.*

All figures drawn by the author at an enlargement of c. 700, and reduced to half size.



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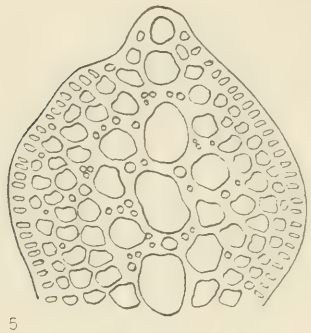

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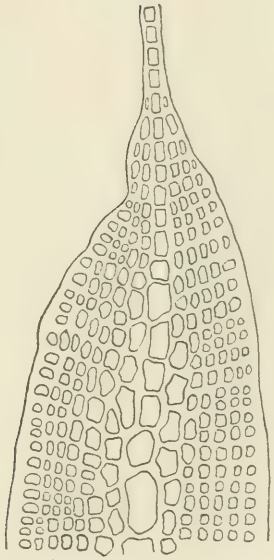

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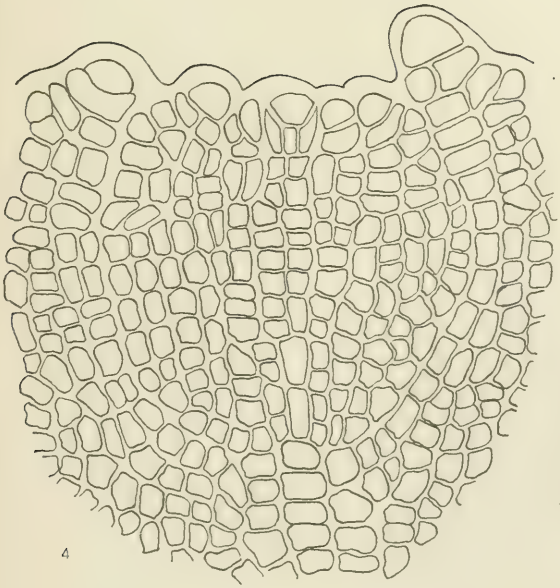

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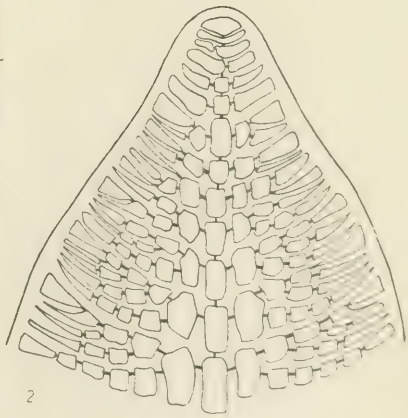

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UNDESCRIBED PLANTS MOSTLY FROM BAJA CALIFORNIA

BY
IVAN MURRAY JOHNSTON

Ephedra peninsularis sp. nov.

Fruticulus intricatus superne dense ramosus, ca. 8 dm. altus; ramis tenuibus, patentibus, numerosis, pallide viridibus; squamis 2, 1.0–1.7 mm. longis, ½–⅔ connatis, apice late triangularis vel obtusis, basi plerumque brunneis incrassatis; spiculis axillaribus solitariis vel geminatis; spicula mascula ovato-oblonga, 5–6 mm. longa; pedicellis 0.1 mm. longis; bracteis 3–4 verticillastris, orbicularibus; perianthio obovato plerumque exerto; staminibus distincte exertis; antheris 5–7, stipitatis vel subsessilibus; spiculis femineis acute ovatis, 6–8 mm. longis; bracteis frutescentibus ovato-orbicularibus, sessilibus, margine scariosis; fructu multo exserto, solitario, triquetro, glabro, castaneo, 5–6 mm. longo.

Type.—Magdalena Island, Baja California, January 12, 1889, *T. S. Brandegee.* Sheet no. 119069 in Herb. Univ. Calif.

This is the common and widely distributed *Ephedra* of Baja California, which ranges over the peninsula from the cape region northward at least to Calmalli and Cedros Island. The only other *Ephedra* that I have seen from the peninsula is the three-bracted *E. californica*, which occurs in the northernmost parts of the territory. I have examined material representing the new species collected by Purpus at Las Animas (269) and Calmalli (6), by Brandegee at Magdalena Bay and Calmalli, by Anthony on Cedros Island (281), and by myself on Coronados Island in the Gulf of California (3757). Brandegee (Proc. Calif. Acad. Sci., II, 2:205. 1899) reports the plant as *E. nevadensis;* but the ranges of *E. nevadensis* and *E. peninsularis* are separated by a broad geographical hiatus, and, furthermore, the two species are quite distinct morphologically. The latter species differs from *E. nevadensis* in its more slender and limber stems, shorter and

more united bracts, and fewer scaled aments. In the development of the leaf scales the new species is remarkably like *E. pedunculata*, but that species differs in its long reclining stems, long pedunculate ovulate aments, and in its far removed range. The short, much united leaf scale is a character which will distinguish *E. peninsularis* from most North American species.

Stenophyllus nesioticus sp. nov.

Annuus multicaulis; foliis filiformibus, 2–6 cm. longis, minus quam 1 mm. latis, glabris, sulcatis, scabridis, quam culmo multo brevioribus, vaginarum faucibus pilosis; culmis tenuibus, levibus, numerosis, obscure trigonis, prope apicem sulcatis, 1–6 dm. altis; involucri bracteis inconspicuis, quam spiculis plerumque brevioribus, 4–12 mm. longis, exterioribus 2 interiores multo superantibus, anguste dilatatis; spicularum bracteis ovato-lanceolatis, 3–6 in capitulum densum sessile, 4–6 mm. longum, 8–12-florum congestis, badiis; glumis late ovatis, 25–30 mm. longis, 3-nerviis, extus tenuiter scabrido-pubescentibus, margine plerumque fimbriatis; glumis inferioribus mucronatis; staminibus 3; antheris lineari-lanceolatis, ca. 1.7 mm. longis, apice mucronatis, loculis basi pilosis; stylo trifido, quam achaenium maturum triplo longiori; nucis obovatis, ca. 1 mm. longis, albis, trigonis; stylis coronatis, angulis levibus prominentibus, faciebus transverse rugosis.

Typo.—San Benedicto Island, Revillagigedo Islands, May–June, 1897, *A. W. Anthony 317*. Sheet no. 201076 in Herb. Univ. Calif.

A species most nearly related to *S. Warei* Britt. (*Isolepis Warei* Torr.) of Florida, and to *S. Sellowiana* n. comb. (*Is. Sellowiana* Kunth, Enum. 2:208. 1837) of Brazil. From *S. Warei* (cf. Clarke, III, Cyperac. t. 45, figs. 4–7. 1909) it differs in its darker and fewer spikelets, narrower scales, and longer fringed involucral bracts; from *S. Sellowiana* it differs in its fewer spikelets, and longer involucral bracts which are neither obtuse nor ovate-oblong. From descriptions it appears to be near some exotic forms, notably *F. cinnamomea* (Clarke) of Africa (cf. Clarke in Thiselton-Dyer, Fl. Trop. Africa, 8:432. 1902). The new species is apparently restricted to the Revillagigedo Islands, which lie three hundred to four hundred miles southerly from the tip of Baja California. I have seen material, collected by Anthony and by Barkelew, from San Benedicto, Clarion, and Socorro islands. The plant is mentioned as "Fimbristylis sp." by Brandegee (Zoe, 5:27–28. 1900) and by Vasey and Rose (Proc. U. S. Nat Mus., 13:145–149. 1891).

Viscainoa geniculata var. **pinnata** var. nov.

Folia pinnis 3–5 pinnatis.

Type.—San Raimonda Creek, Baja California, April, 1889, *Brandegee.* Sheet no. 109442 in Herb. Univ. Calif.

Viscainoa geniculata is so constant throughout most of its range that this very pronounced variant deserves some recognition. It has been detected in only a single locality and perhaps represents only a local race. It is of interest as its leaves are similar to those of the near related genus Chitonia. The type collection made at San Raimonda Creek has definitely pinnate leaves which have a rhachis 1–3 cm. long; and 3–5, distinct, spaced, oblong or lance-oblong pinnae 12–25 mm. long. A tendency toward the variety is found in *Orcutt 1344* from Rosario (Herb. Univ. Calif. no. 109445), which has a vigorous shoot on which two leaves are parted, although the rest of the collection has its leaves entire.

Condalia Parryi var. **microphylla** var. nov.

Folia parva, minus quam 1 cm. longa; fructu quam eo speciei minori.

Type.—Las Huevitas, Baja California, May 19, 1889, *Brandegee.* Sheet no. 80099 in Herb. Univ. Calif.

Collections made on Cedros Island by Palmer (752) and Brandegee, and one made at Las Huevitas by Brandegee are similar to one another, but differ from the forms of *C. Parryi* which occur in Alta California in their conspicuously smaller leaves, stouter habit, and slightly smaller fruit.

Euphorbia dentosa nom. nov.

Euphorbia setiloba dentata Engelm.; Boiss. in DC., Prodr. 15²:44. 1862.

Annual; stems very slender, 1–3 dm. long, villous, internodes 15–30 mm. long; leaves opposite, obliquely ovate, rather thin, glabrous or sparsely villous, finely serrate, light green above, glaucous below, 5–14 mm. long, 4–12 mm. wide, petioles 1–2 mm. long, stipules subulate; involucres solitary or in close clusters, long villous, about 0.9 mm. high, on peduncles 0.5–2.0 mm. long; glands brownish; appendages white, lacerate, 0.3 mm. long, 1.0 mm. wide; seeds ashy, prismatic, 1 mm long, faces transversely wrinkled.

The plant described briefly above has been referred to as a variety of *E. setiloba,* but it seems quite distinct from that species, differing in

habit, in its much larger serrate leaves, and in its southern range. The varietal name used by Engelmann is already employed in *Euphorbia* as a specific name, so that it has been necessary to propose a new one. The species is based on material collected at Cape San Lucas by Xantus. I have studied, and the above diagnosis is based upon collections made by Palmer (34) at La Paz, Grabendörfer at San José del Cabo, and Brandegee at San Felipe; all from the cape region of Baja California.

Euphorbia peninsularis sp. nov.

Perennis; caulibus 1–4 dm. longis, ut videtur ascendentibus vel prostratis, brunneis, laxe dichotomeque ramosis, internodiis 20–45 mm. longis, juvenibus dense tomentosis, vetustis praesertim ad nodos sparsim canescenti-pubescentibus; foliis oppositis, integris subsessilibus, rhomboideis, subfuscis, supra pallidioribus, apice obtusis, prope basis latioribus, 1.5–2.7 mm. longis, 5–12 mm. latis, sparsim breviterque villosis; petiolis 0.1 mm. longis; stipulis lineari-subulatis, ciliatis; involucris in glomerulis foliosis ramos breves terminantibus, ca. 1.5 mm. altis, villosis; pedunculis 0.5–1.0 mm. longis; glandulis 4, transverse oblongis, brunneis, appendicibus petaloideis, albis, conspicuis, 1–2 mm. longis, 2–3 mm. latis; capsula ca. 2 mm. longa, pubescenti; seminibus ovatis, angulis 4 rotundatis, faciebus transverse lateque rugosis, 1.0–1.3 mm. longis, 0.8–0.9 mm. latis.

Type.—San José del Cabo, Baja California, January, 1901, *Purpus 325*. Sheet no. 178322 in Herb. Univ. Calif.

The species here described is very distinct and appears to have no immediate relatives. Its large oblongish leaves at first glance suggest the species of the section Hypericifoliae, but its real relationships are in the section Chamaesyce. It may possibly be related to *E. leucophylla*, but that species, while resembling it much in structure and disposition of the involucres, as well as in general habit, has smaller rounded ovate leaves with conspicuously dentate margins. The outstanding features of the plant are its large entire brownish subsessile leaves and tomentose young stems. Besides the type, I have seen an identical plant collected at the type locality by Brandegee (535).

Euphorbia podagrica sp. nov.

Annua; caulibus prostratis, glabratis, 10–15 cm. longis, internodiis 6–10 mm. longis, nodis turgidis; foliis numerosis, oppositis, oblique ovatis, integris, glabris vel paullo villosis, lamina 2–4 mm. longa et 1.5–3.0 mm. lata, petiolis ca. 0.7 mm. longis; stipulis connatis ocream formantibus caule crescente laceratis; stipularum lobis obtusis vel rudimentariis, apice plerumque villosis; involucris in racemis foliosis,

ca. 6 mm. longis, anguste turbinatis, sparsim villosis, lobis 5 parvis; glandulis 4, brunneis, exappendulatis; pedunculis validis, 0.2–0.5 mm. longis; capsula glabra, 12–15 mm. longa, acute angulata; seminibus prismaticis, levibus vel paullo rugosis, ca. 1 mm. longis.

Type.—Washes at Gold Mountain, Nevada, 1898, *Purpus 6437*. Sheet no. 110920 in Herb. Univ. Calif.

Besides the type, I have seen collections of this species from Wilmont, Arizona (*Thornber 341*), from near Holtville, California (*Parish 8087*), and from Imperial County, California (*Wales 8*). The plants of the Californian collections are villous throughout, but those of the other collections are glabrate. The outstanding characters of *E. podagrica* are its annual prostrate habit, knobby stem nodes, entire leaves, and small involucres with reduced unappendaged glands. It seems to come nearest to *E. glyptosperma*, but that species has oblong serrate leaves, unthickened stem nodes, and seeds differently roughened.

Securinega capensis sp. nov.

Fruticulus laxe ramosus, dioicus, ca. 1 m. altus; caulibus rigidis, cinereis praesertim ad ramos juvenes; ramis vetustis breviter calcaratis, foliis oblanceolatis, plerumque fasciculatis, 7–15 mm. longis, 3–4 mm. latis, glabris, subtus manifeste costatis, obscure venosisque; petiolis ca. 1 mm. longis; floribus masculis 2–3-glomeratis; pedunculis strigosis, ca. 1 mm. longis; pedicellis glabris, 2.5–5.0 mm. longis; sepalis 4–5, ovatis; staminibus 5, ca. 2 mm. longis, circa discum lobatum positis; floribus femineis paucis, pedicellis brevibus validis; fructibus juvenibus strigoso-canescentibus; stigmatibus 3, recurvis, 1 mm. longis, apice dilatatis complanatisque; ovario triloculari, loculis interdum biovulatis; fructu brunneo, tenuiter pubescenti, manifeste lobato, diametro ca. 9 mm., globoso-oblongo, pedicellis 3–6 mm. longis.

Type.—West side of cape region, Baja California, October 22, 1893, *Brandegee*. Sheet no. 110393 in Herb. Univ. Calif.

Securinega capensis is a near relative of *S. fasciculata* comb. nov. (*Bernardia fasciculata* Wats., Proc. Am. Acad., 18:153. 1883) and has been referred to that species by Brandegee (Zoe, 4:405. 1894). It differs, however, in the size of its leaves and in the shape and size of its fruit. The new species is known only from the cape region of Baja California, whence I have seen *Brandegee 536* from San José del Cabo, and Brandegee's collection of October, 1893, from the "west side of the cape region." The congener *S. fasciculata* has long remained under Bernardia where Watson first placed it with a query. But there is no doubt that this past treatment is unsatisfactory, for

the plant has two ovules in each cell of the ovary, and so belongs to the Phyllanthoideae (as Brandegee has pointed out), and not among the Crotonoideae.

Tetracoccus Hallii Brandg. (Zoe, 5:229. 1906) is very close to *S. fasciculata* and I am in some doubt as to its distinctness. The association of *T. Hallii* with the very different *T. dioicus* does violence to natural relationships, for not only do the plants differ in the number of cells to the ovary, but in sepal number and shape, in pubescence, and in shape and position of leaves. The opposite leaves in *Tetracoccus dioicus* clearly show a relationship to the alliance called the Toxicodendrinae by Pax (E. & P., Nat. Pflanzenf., 3^5:31. 1896), whereas the characters of *T. Hallii* evidently relate it to Phyllanthinae as defined by Pax (*op. cit.*, 17). If one is to accept the character evaluations maintained by the master workers in the Euphorbiaceae, it is impossible to leave *T. Hallii* congeneric with *T. dioicus*. Among the described genera the plant seems to fit better in Securingea, and so it seems best to call it *S. Hallii* n. comb. *Securinega Hallii*, *S. fasciculata*, and *S. capensis* form a small natural group in the section Fluggea, and though suggesting *S. ramiflora* probably are to be associated with *S. acidothamnus*: the relationships, however, are not close, and the three species differ from other Securinegae in habit and caruncular seeds. The following key contrasts the characters of *Tetracoccus dioicus* and the three Securinega species discussed.

Ovary 4-celled; sepals on female flowers linear, becoming 3–5 mm. long; leaves linear, opposite; plant glabrous throughout.....**Tetracoccus dioicus**

Ovary 3-celled; sepals on female flowers triangular or ovate, becoming 2 mm. long; leaves spatulate or oblanceolate, alternate; young branches and fruit pubescent

Fruit globose-oblong, rather strongly lobed, becoming 9 mm. in diameter, flattened at base; leaf blades 7–15 mm. long, 3–4 mm. wide.....**Securingea capensis**

Fruit oblong, weakly lobed, becoming 5 mm. in diameter, sunken in deeply at base; leaf blades 9 mm. long or less, becoming 3 mm. wide

Sepals 6; male flowers on pedicels 5 mm. long, Californian.....**Securingea Hallii**

Sepals 5; male flowers on pedicels 2 mm. long, Mexican.....**Securinega fasciculata**

Mentzelia hirsutissima var. **nesiotes** var. nov.

Corolla aurantiaca; foliis 1–2 cm. latis, crasso-dentatis.

Type.—San Benito Island, March 28, 1897, *T. S. Brandegee*. Sheet no. 138558 in Herb. Univ. Calif.

Typical *M. hirsutissima* Wats. is known only from the type locality on Angel de la Guardia Island, where in 1921 I re-collected it in a small-flowered form. The species differs from *M. involucrata* in its more narrow green, instead of broad scarious, bracts. There are two varieties of *M. hirsutissima*, one from the peninsula of Baja California, and the other, the one here described, from the west-coast islands. The first variety may be called *M. hirsutissima stenophylla* n. comb. (*M. stenophylla* Urb. & Gilg, Nov. Act. D. Akad., 76:80. 1900). In the species and in the variety *nesiotes*, the middle lobe of the anthers equals or exceeds the lateral lobes, but in the variety *stenophylla* the middle lobe is greatly elongated and twice the length of the lateral lobes. The variety *stenophylla* ranges over the northern third of Baja California. The variety *nesiotes* is known only from San Benito, Natividad, and Cedros islands, from which it has been reported as *M. involucrata* (Zoe, 5:22–24. 1900); it is characterized by its orange corolla, and not very thick coarsely toothed leaves. Possibly the variety *nesiotes* is the basis of the report of *M. tricuspis* from Cedros Island (Urb. & Gilg, *op. cit.*, 80), but *Palmer 712*, cited as the basis of that report, is determined as *M. adherens* by Vasey and Rose (Contr. U. S. Nat. Herb., 1:16. 1890).

Mentzelia involucrata var. **megalantha** var. nov.

Petalis 3.5–4.5 cm. longis.

Type.—Near Salton, Riverside County, California, April 21, 1905, *Hall 5839*. Sheet no. 68744 in Herb. Univ. Calif.

The species is characterized by its large, white, scarious, green-margined floral bracts. In California it is most common in the Colorado Desert from which it extends eastward into Arizona. The species occurs in two forms, which are sharply separated by their flower size. The typical form of the species is the small flowered plant, with petals 1.5–2.5 cm. long, for in the original description Watson gives the length of the petals as "an inch." The flowers in the variety *megalantha* are very large and much resemble those of *M. laevicaulis*. The variety ocurs only in the Colorado Desert, where, judging from the relative amounts of material, it is less common than the species.

Mentzelia tricuspis var. **brevicornuta** var. nov.

Lobis lateralibus antherarum oblongis, rotundatis, minus 0.5 mm. latis.

Type.—Barstow, San Bernardino County, California, May 14, 1903, *K. Brandegee*. Sheet no. 108381 in Herb. Univ. Calif.

The species is unique in the section Bicuspidaria because of its pedicellate flowers and petiolate leaves and bracts. It ranges from Utah and Arizona into the eastern part of the Mohave Desert in California. The variety *brevicornuta* is the form which the species assumes near its western limit in the vicinity of Barstow. In typical *tricuspis* the lobes of the filaments are linear and 2 mm. long at least; but in the new variety the lobes are short oblong and only about 0.5 mm. long. *Mentzelia tricuspis* has been frequently misidentified as *M. reflexa* Cov., no doubt because its fruits are reflexed and appear much as those illustrated in Coville's (Contr. U. S. Nat. Herb., 4:108, t. 9, 1893) plate of *reflexa*. *Mentzelia reflexa* is not even closely related to *M. tricuspis* and can be recognized by its smaller corollas and unlobed filaments.

The species and varieties of Mentzelia which make up the section Bicuspidaria may be distinguished by the following key.

Flowers pedicellate; upper leaves and floral bracts petiolate
  Lateral lobes of anthers linear, acute, 2 mm. long or more.....**M. tricuspis**
  Lateral lobes of anthers oblong, rounded, about 0.5 mm. long.....
M. t. brevicornuta

Flowers, upper leaves, and floral bracts sessile
  Floral bracts white and scarious, with green midrib and margin
    Petals small, 1.5–2.5 mm. long.....**M. involucrata**
    Petals large, 3.5–4.5 mm. long.....**M. i. megalantha**
  Floral bracts green, not at all scarious
    Middle lobe of anthers equalling or shorter than lateral ones
      Corolla pale yellow; leaves 7–12 mm. wide, thickish, deeply lobed.....
M. hirsutissima
      Corolla orange-yellow, leaves 10–20 mm. wide, thinner, coarsely toothed
M. h. nesiotes
    Middle lobe of anthers twice the length of lateral ones....**M. h. stenophylla**

Cryptantha inaequata sp. nov.

3–4 dm. alta, caulibus ramis laxe ramosis; foliis planis, linearioblanceolatis, 2–4 cm. longis; inflorescentia laxe racemosa, 4–12 cm. longa; calyce fructifero 2.5–3.0 mm. longo, lobo abaxillari maximo hispidissimoque; pedicellis brevibus denum 0.1 mm. longis; nuculis 4, heteromorphis, subtrigono-ovatis, acute marginatis; nuce larga quam gynobasi longiore, 1.7 mm. longa, sulco supra medium clauso inferne dilatato areolam triangulam formante.

Type.—Pleasant Cañon, Panamint Mountains, California, May 10, 1906, *Hall & Chandler 6925.* Sheet no. 100917 in Herb. Univ. Calif.

This is a species most nearly related to *C. racemosa,* but differing from it in its sessile or very short pedicellate calyx, and in the shorter lived herbaceous stems. Excluding *C. pterocarya,* it differs with *C. racemosa* from all other winged fruited species in having heteromorphous nutlets. The plant is known only from two collections in the eastern part of the Mohave Desert of California.

Cryptantha maritima var. **pilosa** var. nov.

Speciei similis sed calyce pilis longe patentibus praedito.

Type.—On stony ridges at Los Angeles Bay, Baja California, 1887, *Palmer 551.*

This well marked variant, characterized by its pilose calyx lobes, is frequent in the deserts of southeastern California. From Logan, Nevada, where collected by Kennedy, it ranges south to Santa Agueda (*Palmer 2142*) in Baja California.

Cryptantha racemosa var. **lignosa** var. nov.

Fruticosa, laxe ramosa, 2–4 dm. alta; ramulis floriferissimis; inflorescentia laxe racemoso-paniculata, per omnes partes plus minus aequaliter distributa.

Type.—Panamint Cañon, Inyo County, California, May 15, 1906, *Hall & Chandler 7034.* Sheet no. 100892 in Herb. Univ. Calif.

Typical *C. racemosa,* which ranges south into Baja California from the southern part of the Colorado Desert, is replaced in the Mohave Desert and in the northern part of the Colorado Desert by a slender diffusely branched very floriferous form, which I am here naming variety *lignosa.* The new variety differs from the species in its loosely racemose-paniculate, instead of racemose, inflorescence, and in having its flowers distributed more or less completely through the plant and not confined to a terminal cluster or a peripheral belt. Piper apparently recognized the two forms of *C. racemosa,* but in attempting to name them described the wrong plant; his *C. suffruticosa* (Proc. Biol. Soc. Wash., 32:42. 1919) being typical *C. racemosa.*

Houstonia australis sp. nov.

Perennis glabra; caulibus e radice multis, erectis, simplicibus vel interdum ramo uno, teretibus, 30–45 cm. altis; foliis linearibus, acuminatis, 25–45 mm. longis, 1–2 mm. latis, valde costatis, oppositis; petiolis attenuatis; stipulis minutis, 2–4, setiferis; corolla hypercrateriinfundibuliformi, 7–9 mm. longa ut videtur rufa, tubo 3–5 mm. longo; faucibus 1.5 mm. longis, tubulatis vel tubulato- infundibuliformibus; lobis oblongis vel ovato-oblongis, 2.5–3.0 mm. longis, intus villosis; antheris exertis; stylo incluso; hypanthio 0.5–0.7 mm. alto, quando frutescente fere 2 mm. alto; capsula globosa, ½ infera, diametro 2 mm.; seminibus 0.3–0.6 mm. longis, ovatis, concavo-convexis, scrobiculatis, brunneis.

Type.—Bmorama, Baja California, September 27, 1899, *T. S. Brandegee*. Sheet no. 201101 in Herb. Univ. Calif.

Houstonia australis is known only from the mountains of the cape region of Baja California whence it has been reported by Brandegee as *H. brevipes*. The nearest relative of *H. australis* is *H. angustifolia*, which has a far removed range, oblong instead of globose fruits, and smaller corollas which vary between 4 and 7 mm. instead of between 7–9 mm. in length. *Houstonia brevipes*, which is lacking in the cape region, has larger (9–15 mm. long) flowers, and narrower (under instead of over a mm. wide) sessile rather than short petiolate leaves.

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THE MORPHOLOGY, DEVELOPMENT, AND ECONOMIC ASPECTS OF SCHIZOPHYLLUM COMMUNE FRIES

BY

FREDERICK MONROE ESSIG

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I. INTRODUCTION

The peculiar split character of the gills of *Schizophyllum* called the attention of botanists to this genus in comparatively early times. Mention of this fungus appeared in Dillenius' "Catalogus plantarum sponte circa Gissam nascentium" more than 200 years ago. Since that time (1719) it has been frequently collected and described, and in the last quarter-century has been reported to be of considerable economic importance, but the literature upon the common *Schizophyllum* is singularly fragmentary and incomplete. Early mention was in the form of collection notes or brief descriptions of the dried sporophores. Many of these appeared in print between the time of Dillenius and the latter part of the 19th century.

In 1884 W. G. Smith found *Schizophyllum* growing upon ensilage. This is the earliest mention of its economic importance in available literature. Since this article appeared *Schizophyllum* has been reported as parasitic upon a large variety of hosts, but papers relating to the exact nature of the parasitism are not to be found.

There is also very little published concerning the microscopic structure of the sporophores or vegetative hyphae. A few sentences and one figure in Buller's "Researches on Fungi" (1909) give an inkling as to the structure of the hymenium and hyphae composing the gills. No mention or illustration of contained protoplasmic structure has been found. Rumbold (1910) described and featured the walls of the vegetative hyphae, but did not mention the cell contents.

The literature upon the morphology of the sporophores, however, is much more complete than that upon the microscopic structure. Early descriptions were mostly confined to the structure of desiccated specimens. Hasselbring in 1907 called attention to the development of the sporophores and the peculiar relationship of the hymenophore to the pileus and stipe. Buller (1909) gave a full description of the mature sporophores, origin of the secondary lamellae, marginal splitting, and incurving of the lamellar plates. Adams (1918) described the origin and development of the lamellae. The phenomena he describes, however, do not agree with the phenomena displayed by sporophores growing in their normal habitat on the University of California campus.

This paper is presented in an effort to give a more accurate and complete description of the sporophores; a description of the microscopic structure of the hyphae which go to make up the sporophores and the vegetative mycelium; an account of the origin and development of the gills as found in specimens growing in the field at Berkeley, California; and a report on the economic aspects of the fungus.

According to Saccardo (1887–1895), there are twelve species of *Schizophyllum,* all of them being tropical or subtropical except *S. commune* Fries, which is distributed throughout the northern and southern temperate zones. Hennings (1898) stated that all of the twelve forms described probably constituted only two or three distinct species, and this view seems to the writer to be more nearly correct. The original work reported in this paper is confined entirely to *Schizophyllum commune* Fries,[1] but in the table of geographical distribution and the list of host plants reference is made to the genus as a whole, as it is extremely difficult to distinguish between the one species of the temperate zones and the several tropical species described.

II. MATERIAL AND TECHNIQUE

The sporophores studied came from three sources:

1. Decayed wood in the field.
2. Decayed wood kept in moist chambers in the laboratory.
3. Specimens from the Herbarium of the University of California.

The specimens obtained from the field were collected over a period extending from September, 1917, to February, 1920. They were found growing under natural conditions upon the wood or bark of *Acacia* sp., *Quercus agrifolia,* and *Umbellularia californica.* In all several hundred specimens have been collected, ranging in age from apparently a few hours to two years, and in size from less than 1 mm. to 5 or 6 cm. in diameter. More than a hundred specimens of very young sporophores were obtained during the autumn of 1919 from a single log of *Umbellularia* partly imbedded in gravel along a small creek near the laboratory.

As an experiment short sections of small trunks and branches of trees infected with *Schizophyllum* were placed in shallow pans of water and covered with bell jars. Air was admitted by supporting the bell

[1] For a complete list of synonyms see Greville (1824) and Murrill (1915). The most important are *Agaricus alneus* Linnaeus, *Schizophyllum alneum* Schroeter, *Schizophyllus alneus* Murrill.

jars so that the lower edge did not quite touch the surface of the water. Under these conditions sporophores could be induced to grow throughout the year, new ones appearing successively as the mature specimens were removed. In this way the development of the sporophores could be watched from day to day and compared with conditions found in the field. It might be stated here that at no time was there any essential difference between specimens found in the field and those grown in moist chambers in the laboratory. The moist chambers also furnished an excellent opportunity for the study of regeneration phenomena.

In the third source of material, the Herbarium of the University of California, specimens from many localities in California are preserved, as well as some from Whidbey Island, Washington; from Ontario, Canada; and from France. These sporophores were used for comparison with respect to general morphological characters.

In the matter of technique no claim is made for originality. It was found at the beginning of the work that the processes used in the treatment of the fleshy fungi did not give satisfactory results when applied to *Schizophyllum*. After experimenting with many methods those outlined below were found to be the best suited for use with this fungus.

The killing and fixing agent used for the young sporophores was a 70 per cent solution of alcohol with 6 c.c. of commercial formalin added to each 100 c.c. of the alcoholic solution. This not only killed and fixed the material but preserved it indefinitely. Spores were caught in a film of albumen fixative on a slide and fixed in 100 per cent alcohol, thus hardening the fixative and fastening the spores to the slide.

Most of the sectioning was done on a rotary microtome, the material being frozen in a solution of gum arabic (compare Gardner, 1917). Some of the specimens were imbedded and sectioned in paraffin, but this method did not give good results, as the material became hard and difficult to section. The sporophores for the study of early developmental stages were sectioned individually, and all the sections from a single specimen were preserved in a vial. From these vials the sections were poured into shallow dishes where all could be seen. Only those sections cut at or near the median plane were selected for mounting. Albumen fixative was used to fasten the sections on the slide. Great care was used in orienting the imbedded sporophores before sectioning, as oblique sections through the revolute hymenial margins

lead to entirely erroneous interpretations of the structure of the sporophore. Thus sections cut obliquely through specimens with well developed "gills" which can be seen unmistakably with the unaided eye appear as though the hymenium lined a series of chambers, or as if the "gills" in the middle of the section were normal, with "hymenial chambers" at each edge. Certain sections cut in this manner corresponded in many ways to figures given by Adams (1918). Material for young developmental stages was sectioned from 20 to 25μ in thickness so that the sections would remain entire. For cytological work the sections were cut 5 and 10 micra thick. Sections as thin as 5 micra will not hold together well, so that, for the finer structure, it was necessary to use only fragments.

Flemming's triple stain was used for some sections, but was not so satisfactory as safranin alone. Using a two-minute period in a 3 per cent solution of safranin in 50 per cent alcohol and washing out rapidly, a fair differentiation was obtained. The nuclei stain deep red, the cytoplasm a very light pink, and the cell walls an intermediate shade. All efforts to make the nuclei stand out more clearly by counterstaining resulted in failure. For staining spores, a 48-hour period was needed, as in a shorter period the stain would be almost entirely removed in the washing-out and dehydrating operations preceding clearing and mounting. The sections and spores were cleared in xylol and mounted in Canada balsam.

III. MORPHOLOGY

1. GENERAL CHARACTERISTICS OF THE SPOROPHORES

Schizophyllum is distinctly a xerophyte. The sporophores are found in either of two conditions:

1. In dry weather the sporophores are desiccated, hard, and somewhat brittle (fig. 1, pl. 51). The margin of the pileus is curved inward, decreasing the width of the sporophore about 25 per cent. Each hymenial plate is incurved on the side toward the hymenium. The hymenial surface is hidden and protected. Only the villous sterile surface of the hymenial plates can be seen from the lower side. There is no discharge of spores. This is an inactive period.

2. In moist weather the sporophores take up water and become flexible and leathery in consistency. The pileus margin is only slightly curved downward. The gill plates unroll and extend vertically downward, or nearly so (fig. 2, pl. 51). Spore discharge begins about an

hour after the sporophores are moistened, and continues for a maximum period of about two weeks. However, under natural conditions the period is usually shorter, as the spores cease to fall as soon as the sporophores become dry. Growth takes place, the most actively growing region being at the pileus margin and at the edge of each gill plate. Specimens are naturally most commonly collected when in a dry condition.

The form of the fruit bodies varies greatly, depending in great part upon the position of the surface of the substratum. Thus the sporophores growing upon the under surface of a piece of wood are quite different in form from those found upon the upper surface, and those growing from a vertical surface differ from both of the preceding; but for every one of these three positions the form is fairly constant.

The diversity of form is due to the peculiar organization of the sporophore, the stipe being attached to the upper surface of the pileus, with the hymenophore upon the opposite side of the pileus away from the stipe. Thus *Schizophyllum* differs from all other stipitate members of the Agaricaceae so far studied. This difference was conclusively demonstrated by Hasselbring (1907), who grew the sporophores upon a klinostat. He showed that, when not influenced by the force of gravity, the stipe was always attached near the center of the pileus, but on the opposite side from the "gills." This unusual organization, according to De Bary (1887), is also possessed by *Cyphella*, a member of the Thellephoraceae.

The form which Hasselbring found is the one assumed by fruit bodies growing in nature from the under surface of the substratum. There is a stipe, which is usually short, attached to the center of the upper surface of the pileus. The sporophore is shaped like a broad funnel or bell, the hymenium lining the inner, and also the lower, surface (fig. 1, pl. 52). On a vertical surface the form of the sporophores depends in great part upon the length of the stipe (fig. 2, pl. 52). If this structure is short, it is attached to the pileus near the edge, and the sporophore is ear-shaped. If the stipe is long, it may be curved downward at the outer end and be attached to the pileus near the center, as in specimens grown upon an under surface. Then the shape is that of a curved trumpet. In the ear-shaped forms the stipe is so short that it cannot curve downward, so that the upper edge of the young sporophore is stimulated by gravity (as shown by Hasselbring) to grow more rapidly than the lower edge. Thus the hymenium is

brought into a more advantageous position for spore discharge. On an upper surface the stipe is attached to the pileus at the very edge (fig. 3, pl. 52). The lower edge of the young trumpet-shaped sporophore never develops. The gill plates radiate outward from a place near the attachment of the stipe.

The sporophores are borne singly or in groups. The groups may contain from a few to several scores of specimens attached to each other at the base of the stipe. Sometimes more than one sporophore grows upon a single stipe, but such an occurrence is rare. Only certain members of a group reach maturity, a large percentage never developing beyond a very early stage.

2. DESCRIPTION OF THE MATURE SPOROPHORE

The shape of the individual sporophore varies from broadly bell-shaped with a centrally attached stipe to ear- or racket-shaped with the stipe attached to the edge of the pileus. The edge of the pileus may be entire or more or less deeply lobed. If the lobes are large and deep, they may have secondary lobing. The size of the mature sporophores ranges from 2 mm. to 5 cm. in length and from 3 mm. to 6 cm. in width.

The color of the pileus may be silvery or velvety white, gray, or cream colored. The sterile surfaces of the hymenial plates are a dark gray with often a purplish tint. The hymenium is a shiny brownish-gray. There is a considerable variation in the color of all parts of the fruit bodies, depending upon the age and whether they are wet or dry.

A stipe is usually, but not always, present. Its presence and length depend upon the amount of moisture in the substratum and atmosphere at the early stages of growth, a maximum amount of moisture inducing a greater growth in length. The length varies from 1 mm. to 2 or 3 cm. The form is cylindrical. The stipe rarely attains a width of more than half a centimeter.

The pileus is covered with a dense mass of thick-walled hyphae. If these hyphae are vertical and remain free from each other, the surface appears velvety. If they are agglutinated into groups at the upper ends, the surface is rough and scurfy. If the upper ends form a horizontal layer, the surface has a silvery sheen. The depth of the hyphal covering varies from 1.5 to 2.5 mm. The pileus is made up of thick-walled, septate hyphae. These are closely packed together,

but do not in any case constitute a pseudoparenchymatous tissue. The upper layer of the pileus flesh is pigmented brown.

The lamellar plates extend downward from the pileus (fig. 22, pl. 52). They are arranged in pairs; each pair, with the sterile, hairy surfaces together, giving the appearance of a lamella. Each plate, however, is independent of the other to a certain degree, and may vary from it in size and shape. A hymenial plate may attain a depth of 3 mm., the depth depending entirely upon the number and length of the growing periods following the origin of the plate, for growth is continuous throughout the duration of favorable conditions. Each plate exhibits a growth region at the margin, which, after the earliest stages, is continuous with and similar to the margin of the pileus. Since the plates arise successively in pairs, a great many different ages and sizes may be found in the same mature sporophore.

The hymenium either covers a much divided single area or is separated into several different areas in the same sporophore, as in plate 53. The elements in the hymenial layer are closely crowded together, and in old specimens tightly adhere to each other, so that a large area of the hymenium may be removed from the subhymenial layer without separating the basidia from one another.

3. MICROSCOPIC STRUCTURE

The study of the microscopic structure of *Schizophyllum* presents considerable difficulty. Upon dehydration the sporophores become hard and brittle, so that the paraffin method of obtaining sections is impracticable. When, by using other methods, sections are obtained, it is found that the hyphal walls are thick, the segments extremely long, and that the nuclei are small and difficult to differentiate by staining.

The vegetative hyphae commonly branch, but not with great frequency. The branching rarely occurs at or near a septum, but usually takes place about the middle of a segment (fig. 1, pl. 54). The hyphae are of two sizes, one having a diameter of 3 to 5μ, and the other being only about 1 or 2μ wide. The finer hyphae are particularly abundant when the mycelium is grown upon artificial media, but are also found to some extent in wood. The hyphae are often covered with small tubercles, as was described by Brefeld (1889) in *S. lobatum* and Miss Rumbold (1910) in *S. commune*. This seems to be a distinctive character. The function of these lateral projections (fig. 2, pl. 54) is not

apparent from their structure. It is possible that they aid in the absorption of food materials, since they closely resemble haustoria in shape and are found only on those hyphae which are purely vegetative. Clamp connections (fig. 1, pl. 54) are found at more than half of the septa in actively growing mycelium. They have been observed upon the hyphae of members of the Hymenomycetes since the earliest studies of their cell structure. Though they occur in a great number of fungi in this group, their exact function is not understood. Harper (1902) suggested that they possibly facilitated the exchange of food materials between segments, but just how this is accomplished is not clear. The length of the segments varies from about 30μ to more than 200μ, the usual length being about 80μ. The thickness of the wall varies from about 0.1 to 0.5μ. In rapidly growing hyphae there are few vacuoles and these are small. The protoplasm is of fine granular structure and very homogeneous. As the mycelium becomes older the vacuoles enlarge, oil droplets are formed, and many of the cells collapse. There are two nuclei to a segment (fig. 1, pl. 54). They are small and spherical, about 0.3 to 0.5μ in diameter. Their structure is granular. No nucleoli have been seen. The nuclei are usually found about 10 to 20μ apart near the center of a segment. These compare very well with the nuclei in the vegetative hyphae of *Hypochnus subtilis* (Harper, 1902, fig. 1, pl. 1). Maire (1900) found but one nucleus in the "cells" of the mycelium of *Coprinus radiatus.*

The hyphae which compose a sporophore are of several different types. One kind includes those which form the hairy covering of the pileus and sterile surface of the hymenial plates; another makes up the pileus and tramal structure, and the third forms the subhymenial layer. Again, each of these types varies somewhat according to the age and state of development of the sporophore.

The hyphae which cover the pileus and sterile surfaces of the hymenial plates are composed in nearly all cases of but a single segment, which may be as long as 3 mm. These hyphae are of a fairly uniform size and length (fig. 3, pl. 54). They are irregularly curved and tangled together. The walls are in the younger stages fairly thin, but as development proceeds they gradually thicken until in very old specimens the lumen has almost entirely disappeared. Two nuclei are present in each hypha of the hairy covering. They are similar in size and shape to those of the vegetative hyphae. They are found regularly near the base of the segment.

The filaments which constitute the solid portion of the sporophore are in their younger stages similar to the larger hyphae which make up the vegetative mycelium (fig. 4, pl. 54). As the fruit bodies become older the segments lengthen, and the walls thicken until they are about equal in thickness to the width of the lumen (fig. 5, pl. 53). When the microscope is focused up and down upon thick sections cut transversely across the hyphae it is seen that the filaments are loosely coiled in a fairly regular spiral, some turning clockwise and others counter-clockwise. In old sporophores the hyphae adhere tightly to each other wherever they are in contact. In the earlier thin-walled state the segments are filled with cytoplasm and have two typical, small nuclei This is precisely the situation found by Harper (1902) in *Coprinus ephemerus* and *Hypochnus subtilis*. Clamp connections are numerous, but no spine-like tubercles appear. The protoplasmic contents of the thick-walled hyphae of older sporophores are masked by the walls to such a degree that the number of nuclei present cannot be determined. In *Coprinus ephemerus* (Harper, 1902) there are many nuclei in the old "cells" of the pileus and stipe. Maire (1900) found the same to be true in a large number of the fleshy Agaricaceae which he had examined.

The subhymenial layer is composed of hyphae which are thin-walled, and which retain the characters displayed by all the hyphae in their earlier state. Branching is common, and clamp connections are plentiful. There are two nuclei to each segment. The segments are rich in cytoplasm.

The basidia are borne at the ends of thin-walled hyphae. They are only slightly larger in diameter than the hyphae which bear them. All the elements in the hymenium are similar (fig. 6, pl. 54), that is there is no distinction between potential basidia and paraphyses. Mature basidia project beyond the hymenial surface. The basidia come to maturity in succession, only a few in a relatively large area being found with spores attached at any one time. The basidia measure 5 by 20μ. Each has four long, slender sterigmata and bears four spores. Immature basidia display two nuclei. No fusion of these nuclei has been observed, but in later stages four have been seen. It is therefore presumed that the usual fusion and two successive divisions, as described by Wager (1893), Maire (1900), and Harper (1902), have taken place.

The spores *en masse* are white. When seen with the microscope they are nearly hyaline and of an olive green shade. There is a con-

siderable difference of opinion in the literature as regards the shape and size of the spores. The early writers, such as Fries (1821), Cooke (1871), and Saccardo (1887), stated that they were subglobose, about 2.5μ in diameter. Morgan (1890) called attention to the fact that the spores he had been examining averaged 5–6 by 2.5μ, and wondered if a mistake had been made, or if his were possibly a different species. The possibility of a different species seems unlikely, for later Hennings (1898) and Rumbold (1910) in Europe and Murrill (1915) in America have found them to be oblong, at least twice as long as broad. It is possible that the globular bodies supposed by the early writers to be spores were nothing but the peculiar structures which are shed by the dried sporophores when first they are wetted to obtain a spore print. These bodies and no spores are dropped by old herbarium specimens, which have lost their vitality, when they are moistened. The spores occasionally possess small vacuoles. No oil droplets have been demonstrated. The wall is thin. The spores are densely filled with protoplasm. At shedding time two nuclei are present (fig. 7, pl. 54).

The number of nuclei in the spores of the Hymenomycetes so far examined is either one or two. One was found in the spore of *Hypochnus subtilis* (Harper, 1902), *Amanita vaginata, Tricholoma virgatum,* and *Cantharellus infundibuliformis* (Rosenvinge, 1886), while two were found in *Craterellus cornucopioides, Clavaria vermicularis, Boletus edulis,* and *B. variegatus* (Rosenvinge, 1886). Maire (1900), after studying some thirty species, stated that there might be either one or two nuclei in a spore. In the case of two nuclei, the single nucleus divides as soon as it enters the spore from the basidium, instead of just preceding the first segmentation during spore germination.

Spores germinate readily in water and in a great variety of culture media. The spores first swell to nearly twice the normal size; then a germ tube appears at either one or both ends (fig. 8, pl. 54). The width of the germ tube often approximates that of the spore, and as a result the identity of the spore may soon be lost. The length that the tube attains prior to segmentation depends to a certain extent upon the nature of the culture medium, segmentation occurring earlier when the medium is rich in food materials. In tap water growth ceases about the time the first septum and branch appear. Branching may occur either before or after the first septum is laid down, but it usually occurs about that time.

IV. GROWTH OF THE SPOROPHORE

1. DEVELOPMENT IN GENERAL

The development of the sporophores was early looked to for an explanation of the peculiar pairs of hymenial plates which characterize *Schizophyllum*. Fries (1821) believed that they arose as ordinary gills and were split by drying. This view was again brought forward by Fayod (1889), and still later by Buller (1909). Hoffman (1860) believed the sporophore to be divided into a series of lamellar systems, considering all the secondary gills to belong to the primary hymenial plates which enclosed them. His view was adopted by Winter (1884).

Adams recently (1918) made the statement that each lamella consists "of the adjacent walls of two gill cavities which originate endogenously as tubes in the substance of the carpophore. The gill cavities (tubes) split along their lower edges and lamellae are thus completed."

In Hasselbring's (1907) paper on "Gravity as a Form-Stimulus in Fungi" appears the statement that "they [the young sporophores of *S. commune*] appear as small outgrowths resembling simple forms of *Clavaria*, and attain a length of about one centimeter. Early in their development a cup-like depression appears at the summit, and within this the rudimentary lamellae are formed, radiating from the center."

Two distinctly opposed views have, then, been advanced by Hasselbring and Adams. Adams held that the "gills" originated endogenously as the sides of horizontal tubes which later ruptured at the lower edge and exposed the hymenium, while Hasselbring claimed that the "gills" arose exogenously upon the surface of an apical cup-like depression. It seems unlikely that Buller and the previous writers had access to sporophores in the first stages of development, for they made no statements concerning the early appearance of the fruit bodies. Both Adams and Hasselbring, however, grew the sporophores through all their stages in the laboratory. Adams grew his in flasks on agar media from "immature carpophores collected in the field." Hasselbring caused them to grow from "pieces of a maple branch containing the mycelium—placed on a klinostat."

The writer has had an opportunity to study the origin and development of the sporophores both on a log of *Umbellularia californica*

(California Bay) in the field near the laboratory where more than a hundred sporophores have grown during the autumn and winter of 1919–1920; and in the laboratory where scores of sporophores have appeared upon the wood of *Acacia, Quercus,* and *Umbellularia* in moist chambers. Dozens of the fruit bodies have been sectioned, either longitudinally or transversely.

No phenomena in the course of the development of the sporophores have been observed that in any way approximated those described by Adams (1918) for *Schizophyllum commune.* By cutting oblique sections through small mature specimens his figures 2 to 7 in plate 9 may be imitated with fair accuracy, but these sections cannot permit of such an interpretation as he has given for his sections. The crenatures which he shows in figures 2 to 5, plate 9, are entirely absent in all of the 160 or more young specimens the writer has examined. The sporophores which grew here in the laboratory and in the field developed much as was described by Hasselbring (1907).

The fruit bodies appear first as small, loose tufts on the substratum. These develop into small white woolly projections either short and hemispherical or prolonged into horn-like structures, "resembling simple forms of Clavaria" (fig. 2, pl. 56). The end is either rounded or conical. These small bodies are covered with loose tangled hyphae. Later the apex becomes smooth, slightly darker in color, and covered with shorter hyphae.

Next a single pore appears at the apex (fig. 3, pl. 56), as Hasselbring (1907) found. Early stages which show the origin of this pore have been difficult to distinguish, as it develops within a few hours after the formation of the buttons or horns, and the loose hairs at the apex screen its first appearance. Longitudinal sections at this stage show first a differentiation of the hyphae just behind the apex (fig. 1, pl. 59). This region stains more deeply than the remainder of the section. The growth at this place is accelerated, and, as increase in size takes place behind the apex, the hyphae at the tip are pulled apart (fig. 2, pl. 59). The hyphae beneath the rupture form a palisade layer which extends laterally into a plane surface (fig. 3, pl. 59). The growth then becomes more rapid at the edge of the layer, producing it outward into a saucer-shaped and later a cup-shaped depression. In this stage it resembles a small sporophore of a *Peziza* (fig. 4, pl. 59).

In all cases observed by the writer the so-called lamellae have originated upon the surface of this apical cavity (figs. 4–14, pl. 52),

which surface constitutes the hymenium primordium. This is exactly as described by Hasselbring (1907), but he did not go into detail concerning the placement or development of the hymenial plates. The pore attains a width of from 1.5 to 2 mm. before the appearance of the first pair of plates. Dozens of specimens in the "apical depression" or "peziza" stage have been observed where there was no indication of lamellae. By splitting the specimen in half longitudinally the entire surface of the hymenium primordium may be examined with a hand lens. Microscopical examination of prepared sections fails to disclose any indication of closed chambers or of "gills" before the "lamellae" are plainly visible upon the surface of the hymenium primordium.

The placement of the "gills" may be easily observed in actively growing moist specimens (figs. 4–14, pl. 52). They arise as short, isolated ridges upon the surface of the hymenium primordium. The primary ridges arise successively from a point beneath the attachment of the stipe, and grow outward in a radial direction until they finally unite with the edge of the pileus. The secondary "gills" originate between the gills already developed, but do not extend so near to the stipe as do those already formed. They occupy, as Buller (1909) noted, an isolated, subterminal position within the interlamellar space in which they have been formed. As growth proceeds, however, the distal ends gradually approach the pileus margin and eventually unite with it, as do the primary ridges.

Soon after a "gill" unites with the pileus margin, the pileus becomes split in from the edge, though often this is not disclosed upon the dorsal surface because of the hyphal covering. This marginal splitting is doubtless to some extent hygroscopic, as specimens kept moist from the first are split only slightly, while those subjected to alternate wetting and drying are split farther toward the stipe ends of the "gills," dividing the pileus as well as the hymenium into narrow finger-like projections, the crenatures of Buller (1909).

Occasionally there is an unusual placement of certain "gills." Sometimes they arise at an angle to the radial direction. In this case they frequently remain short and isolated. Often there is a considerable sterile area between the two hymenial plates (fig. 1, pl. 60). This is very commonly found at the stipe end of "gills" in lateral sporophores. Rarely the first few primary gills formed unite with each other and the pileus margin to divide the hymenium primordium into several separate areas, in which the secondary "gills" later are formed (fig. 15, pl. 52).

Upon a superficial examination the "gills" appear to be much branched. This is especially noticeable in dried specimens (fig. 1, pl. 51). The secondary "gills" are not attached to the primary ones, however, but fit in between and beneath them. Branching occurs but rarely, and is the result of the anastomosing of two "gills" in the early stages of development.

2. ORIGIN AND DEVELOPMENT OF THE "GILLS"

The origin and development of the lamellae has been studied in a fairly large number of members of the Agaricaceae. In all of these Atkinson (1916) recognized two general types. In the first, which he called the *"Agaricus"* type, the hyphae form a palisade layer at the roof of a well-developed annular cavity which appears on the under side of the pileus; and from this palisade layer, which is the hymenium primordium, the lamellae grow downward into the cavity. In the second, or *"Amanita"* type, the gills originate as bars radiating out from the stipe to the under surface of the pileus. The origin and development of the "lamellae" in *Schizophyllum commune* is entirely distinct from either of the above types. The gills grow outward from a palisade layer which forms the lining of a single apical depression or cup.

The origin of a "gill" is evidenced in cross-sections in two ways: either a split appears in the palisade layer and the edges grow outward (fig. 6, pl. 56); or a small area of the palisade layer becomes loosened, grows outward a short distance, and then splits in the middle to a point beneath the original primordial layer (fig. 9, pl. 56). In both cases the growth continues in the same manner. The hyphae beneath the edge of the hymenium on each side of the split grow outward rapidly and cause the hymenial edges to turn downward, and by marginal growth a pair of hymenial plates are soon formed (figs. 1–4, pl. 57). Growth continues at the edges of these plates throughout the life of the sporophore, so that in very old fruit bodies some gill plates may be comparatively deep.

Buller (1909), noting the fact that, in cross-sections of the mature specimens, the tramal layer was split to different depths, thought that the "gills" arose entire and were later split due to hygroscopic tensions. This theory had been earlier advanced by Fayod (1889), who claimed that specimens grown under water have entire "gills." In attempting to demonstrate Fayod's statement it was found that sporophores grow with difficulty under water and decay after a few days.

Those "gills" which did arise under these conditions, however, showed no departure from the process as described by the writer above. In all cases observed the plates have been separated at the edges from the very first. In later stages they may be separated only a short distance toward the pileus, or they may be split to any depth in the tramal hyphae or pileus, or even completely through the flesh of the pileus. Each "gill," after it unites with the pileus margin, is split more deeply at the outer end, and the depth decreases toward the stipe end, as does likewise the size of the "gill."

The splitting or loosening of the hymenium to permit the origin of the paired hymenial plates is due to the same tensions which cause the "gills" themselves later to be split to different depths. The addition of new elements to the hymenial layer does not keep pace with the growth of the hyphae beneath the hymenium. When the hymenium has attained a certain width the tension upon the closely crowded elements of the hymenial layer is so great that it is either split longitudinally near the center of the area, or the palisade elements are loosened, grow outward a short distance, and then split. Likewise the gill plates are split apart to different depths due to the tensions set up by these differences in the rate of growth at different regions of the sporophore. The most rapidly growing region is at the margin of the pileus, and, while growth may and actually does take place throughout the sporophore, it decreases in rapidity from the periphery to the place of attachment of the stipe. Thus the gill plates are longer at the periphery, but the difference between the rates of growth of the hymenium and subhymenial and tramal layers is just as pronounced. As a result the hymenial margins are incurved more at the margin of the pileus and the gill plates are gradually drawn apart.

In some young sporophores the two hymenial margins are separated by a considerable layer of sterile surface which is level with the hymenium (fig. 1, pl. 60). In this case there is not even a resemblance to gills.

From the evidence at hand it seems that the so-called "gills" of *Schizophyllum commune* Fries are such by analogy only, being actually two adjacent edges of hymenial areas which arise together, but which become continuous with and are homologous to the margin of the pileus. They increase the area of the hymenium as do gills, and, when in a moist condition, look much like typical gills; but each plate is independent of the other from the first, increasing in size by marginal growth.

3. TAXONOMIC INTERPRETATION OF THE STRUCTURE AND DEVELOPMENT OF THE SPOROPHORES

It was early observed that while *Schizophyllum* was presumed to possess gills, the structures were unique among the members of the *Agaricaceae*. Consequently considerable difficulty has been experienced among systematists in associating this genus with the other members of the family from which it is so distinct.

Fayod (1889) believed it to be precisely like *Panus*, except that in *Panus* the gills were entire. He classified them under the tribe Panoides, and noted a similarity in the geographical distribution of the two genera. Hennings (1898), following Saccardo (1887–1895), placed *Schizophyllum* in the tribe Schizophylleae with *Rhacophyllus*, *Oudemansiella*, and *Pterophyllus*, but stated that the other genera do not seem to belong to this group. Murrill (1915) put it in the tribe Agariceae and subtribe Lepiotanae along with *Marasmius*, *Lepiota*, and other white-spored members of the Agaricaceae.

All these writers have based their classification upon the assumption that the hymenium in *Schizophyllum* is borne upon the surface of lamellae. Since this is not the case—for the hymenophore while quite complex in structure bears a smooth hymenium—the fungus should be placed in the family Thellephoraceae. In this family it resembles *Cyphella* in the organization of the sporophores, for, in this genus, according to De Bary (1887), the hymenium lines the inner and lower surfaces of a funnel-shaped sporophore, the stipe being attached to the opposite side of the pileus from the hymenium (fig. 16, pl. 52). The early stages in the development of *Schizophyllum commune* and *Stereum hirsutum*, likewise, have much in common. In the later stages, however, the hymenium of *Stereum hirsutum* remains entire, and bears no resemblance to the much divided hymenium of *Schizophyllum commune*. Only in the genus *Cladoderris* is there anything comparable to the hymenial plates of *Schizophyllum*. *Cladoderris* is somewhat similar to *Stereum*, but differs in possessing radiating, branched ribs upon the hymenial surface. Some species of *Cladoderris* have the pileus margin much incised. The representatives of the genus *Cladoderris* are chiefly tropical, and are known to the writer only through descriptions and illustrations. From these it seems that there is only a difference in degree between the splitting of the pileus margin in sporophores of *Cladoderris infundibuliformis* Fries (cf. Hennings, 1898) and the marginal division in fruit bodies of *Schizophyllum commune*.

V. ECONOMIC ASPECTS

1. GEOGRAPHICAL DISTRIBUTION

In a discussion of the economic importance of *Schizophyllum* it seems well to go into detail concerning its distribution throughout the world, as any consideration of the amount of damage done must take into account both its distribution and its abundance in any district. Fortunately a great number of statements have been published concerning its collection in various places. In the table below are given by continents the countries or regions in which *Schizophyllum* has been collected or reported, the authority, and the date of publication of the article. The table is representative rather than exhaustive, as only one reference to a locality has been included.

TABLE OF GEOGRAPHICAL DISTRIBUTION

Continent	Place	Authority	Date
Eurasia	England	Cheesman, W. N.	1904
	Scotland	Paterson, R. H.	1877
	Sweden	Linnaeus, C.	1753
	Germany	Hennings, P.	1898
	France	Gueguen, F.	1901
	Italy	Archangeli, G.	1887
	Central Asia	Sorokine, N.	1890
	China	Roumeguère, C.	1879
	Ceylon	Berkeley, M. J., and Broome, C. E.	1871
Africa	Tripoli	Baroni, E.	1892
	Abyssinia	Saccardo, P. A.	1891
	Cape of Good Hope	Berkeley, M. J.	1876
	Africa	Hennings, P.	1891
North America	Canada	Dearness, J.	1896
	Eastern United States	Atkinson, G. F.	1901
	Middle Western U. S.	Heald, F. D.	1906
	Oregon	Griffin, F. L.	1911
	California	Smith, R. E., and E. H.	1911
	Mexico	Patouillard, N.	1887
	West Indies	Massee, G.	1892
South America	Brazil	Averna-Sacca, R.	1916
Australia	Australia	MacAlpine, D.	1902
	New Zealand	Buchanan, J.	1874

The sporophores of the *Schizophyllum* in the field are usually small and inconspicuous. When found they are usually in large numbers within a small area on a log or tree. Only an occasional tree or log displays them in this region (California). Heald (1906) reported that every tree of a small orchard of cherries in Nebraska was infected with the fungus, but this seems to be an extreme case.

2. LIST OF HOST PLANTS

A large number of plants have been mentioned in scientific literature as hosts of the sporophores of *Schizophyllum*. It is not clear in most of these references whether the specimens were found upon living or dead plants. The distinction is of some importance in the consideration of the economic aspects of the fungus. The information in the following table has been obtained from publications, from the spoken word of collectors whom the writer has been fortunate enough to meet, from specimens in the Herbarium of the University of California, and from observations in the field. Dates are given for references to publications only.

TABLE OF HOST PLANTS

Family	Name	Authority	Date
Pinaceae	Yellow Pine (*Pinus ponderosa*)	Stillinger, C. R.	
	Western Hemlock (*Tsuga heterophylla*)	Stillinger, C. R.	
Gramineae	Sugar Cane (*Saccharum officinarum*)	Ray, J.	1896
	Bamboo (*Bambusa* sp.)	Horne, W. T.	
Palmaceae	Royal Palm (*Oreodoxa regia*)	Horne, W. T.	
Juglandaceae	English Walnut (*Juglans* sp.)	Smith, R. E., and E. H.	1911
	Hickory (*Hicoria* sp.)	Dearness, J.	1896
Betulaceae	Alder (*Alnus* sp.)	Linnaeus, C.	1783
	Birch (*Betula* sp.)	Adams, J. F.	1918
Fagaceae	Beech (*Fagus* sp.)	Rumbold, C.	1910
	Oak (*Quercus serrata*)	Roumeguère, C.	1879
	Chestnut (*Castanea* sp.)	Stevens, F. L.	1913
Moraceae	Mulberry (*Morus* sp.)	Prillieux and Delacroix	1893
Lauraceae	California Baytree (*Umbellularia californica*)	Brown, V. S.	
Rutaceae	Oranges and Lemons (*Citrus* sp.)	Smith, R. E., and E. H.	1911
Tiliaceae	Linden (*Tilia* sp.)	Hennings, P.	1898
Aceraceae	Maple (*Acer* sp.)	Hasselbring, H.	1907
Hippocastanaceae	Horse Chestnut (*Aesculus Hippocastanum*)	Gueguen, F.	1901
Rosaceae	Apple (*Pyrus malus*)	Fulton, H. R.	1912
	Pear (*Pyrus communis*)	Baroni, E.	1892
	Cherry (*Prunus cerasus*)	Griffin, F. L.	1911
	Peach (*Prunus persica*)	Camp, A. F.	
	Almond (*Prunus communis*)	Kellogg, E. S.	
Leguminosae	*Pterocarpus indicus*	Kew Bull. Misc. Inf.	1910
	Acacia (*Acacia* sp.)	Seen in the field	
	Hardy Catalpa (*Catalpa speciosa*)	Stevens, N. E.	1912
Rubiaceae	Coffee (*Coffea* sp.)	Averna-Sacca, R.	1916

3. EXTREME HARDINESS OF THE FUNGUS

Schizophyllum is able to persist under very adverse circumstances. Its unusual vitality is displayed in three ways: (1) the sporophores are able to endure long periods of drought; (2) the mycelium can grow upon almost any moist organic substance; and (3) the sporophores possess the ability to regenerate lost parts.

Buller in 1909 called attention to the long period over which the sporophores can retain their vitality. He stated that "whilst in the dried condition a fruit body can retain its vitality for at least two years, and, with intermittent revivals, for at least three years." Later (1912) he and Cameron found that the fruit bodies could endure sudden changes of temperature, suspension in a vacuum, extreme cold, or a long period in darkness. In this respect they resemble certain seeds and mold spores.

A mycelium produced either from spores or pieces of sporophores will grow upon a whole series of substances. Some of the materials upon which the hyphae grow well are such starchy media as potato tubers, corn meal, rice, "Cream of Wheat," and lima beans; sugary media such as beets, prune juice, and grapes; upon agar and gelatin nutritive media; and upon dung, a wood decoction, or dead leaves. Kellogg (1915) grew the fungus from spore to spore, or through all of its life history, upon sterilized potato plugs in glass flasks, showing that *Schizophyllum* can exist in an entirely saprophytic condition. Earlier Rumbold (1910) had produced sporophores on bread from spore cultures, but, although these bore basidia on a definite hymenium, no spores developed.

Experiments have been carried on to determine to what extent the sporophores can regenerate lost parts. The fruit bodies studied were grown upon blocks of *Acacia* wood kept in moist chambers in the laboratory. In one case about one-half of the pileus at the distal ends of mature sporophores was removed by cutting with a sharp knife. Some of the specimens were left in the original position, and others were inverted by reversing the position of the blocks of wood upon which they were growing. Where the mutilated sporophores were left in position growth ceased at the cut edge, but continued in a normal manner, though rather slowly, at the pileus margins to the side. Most of the inverted specimens ceased growth altogether. In one case, however, in a few days the margin at one side began to turn and grow outward in a horizontal direction with the hymenium facing

downward. At the end of 17 days a normal sporophore about 1 cm. in diameter had developed (fig. 2, pl. 60).

In another experiment the entire hymenophore was removed by cutting across the stipe at the distal end. Specimens left in the original position produced new hymenophores in one of two methods. If the stipe was small at the cut end, only one new sporophore, as a rule, developed by the growth of hyphae out through the cut end of the stipe (fig. 3, pl. 60). This developed in the usual way. If the cut end of the stipe was of considerable area, several small sporophores developed. These grew in the usual way except that the hymenial plates arose in position with respect to the old stipe and not as though the separate sporophores were distinct individuals (fig. 18*d*, pl. 52). The sporophores more advantageously placed, that is, at the upper edge of the stipe, grew more rapidly and became much larger than those at the sides. The sporophores might be cut away to within a millimeter of the base of the stipe and still a new sporophore would develop upon the cut end. The specimens used were mature and were shedding spores, but were comparatively young. Thus the sporophores have, at least while still young and fresh, the ability to regenerate practically the entire body.

Stipes with the entire hymenophore removed and in an inverted position in all cases produced either one or several small sporophores upon the cut end, but growth soon ceased. Sections through these specimens showed that they had stopped growing either in the "peziza" stage or after one or two hymenial plates had been formed (figs. 19–20, pl. 52). The inability of the sporophores to develop further in an inverted position is doubtless due to their lack of power to change the polarity of the different parts with respect to the reaction to the force of gravity. That gravity is the form-stimulus was clearly demonstrated by Hasselbring (1907).

4. RELATION OF THE MYCELIUM TO CELLS OF DEAD WOOD

Upon sectioning dead wood it is found that there is an unexpected paucity of mycelium in the tissues infected by *Schizophyllum*. Wood brought in from the field in a dry condition covered with the sporophores may be sectioned and fail to display any mycelium in a large percentage of the sections. In some, however, a few hyphae can be seen.

The hyphae of this fungus are shown by sections to be confined almost entirely to the tracheae of the wood (pl. 61). In some ducts

there may be only one or two, but in others the lumen may be almost filled. In all cases the mycelium varies considerably in size, the walls are thin, and branching is infrequent. The lateral tubercles are present upon the walls of some of the hyphae.

Wherever the mycelium is found in wood in earlier stages of decay there is present a series of small, globular masses of a brown exudate. The mycelium of *Schizophyllum* growing upon artificial media produces a like substance, so that found in the wood is probably produced by the hyphae. In certain regions the droplets are so numerous that the wood is discolored. They account for the black or dark brown layers often seen near the edge of the decayed areas. In regions of advanced decay they have entirely disappeared.

Cross-sections through the limb of a living tree which was infested with the fungus in a narrow area along one side of the limb showed that the infected area extended in a radial direction to the center of the limb. Some pieces of this limb were placed in moist chambers. In a few days tufts of hyphae grew out of the wood at the edges of the infected area near the living wood and only a few scattering threads could be seen in the central part of the discolored tissues. Thin sections also disclose the fact that the greater part of the vegetative mycelium is near the living wood in partially killed limbs or trunks of trees.

The decay is marked at first by a darkening of the tissues. There are dark brown or black layers near the edge of the darkened areas. At later stages delignification sets in, and the decayed areas become straw-colored. The cell walls become softened, but retain their structure for a long period. The mycelium of *Schizophyllum* is frequently found in areas of advanced decay along with the hyphae of other fungi, and it is difficult to determine how much of the decay is due to the work of *Schizophyllum commune* alone.

5. GROWTH UPON FRESH WOOD AND LIVING TISSUES

Freshly cut pieces of Acacia wood were placed in moist chambers and spores of *Schizophyllum* were planted upon different tissues. Acacia wood was chosen because sporophores are found in abundance upon the dead wood of this tree. The pieces of wood were kept moist enough to cause the spores to germinate. The experiment was carried on for two months. At the end of that time it was found that the

hyphae had not penetrated through the fresh, uninjured bark, or cortical tissues, or through the wood tissues in a lateral direction, but had grown through the wood in the direction of the tracheae.

Attempts to prove the parasitism of this organism were made by Gueguen (1901) and Fulton (1912) with negative results. Rumbold (1910) stated that Tuzson (1905), (whose paper is not available) grew the fungus upon fresh (*frais*) beech wood. Kellogg (1915) was not able to demonstrate the mycelium of *Schizophyllum* in the inoculations made upon fruit trees.

In my inoculation experiments young fruit trees of apple, pear, and plum were used. Inoculations were made from agar plates of pure cultures of the mycelium. The limbs of these trees were either split through the center or cut into from the surface to varying depths. A sterile knife was used in the incisions. The mycelium with substratum was transferred to the cut or slit surface and the wound was tied up with string and covered with waxed paper, a layer of wet absorbent cotton, and another layer of waxed paper. The purpose of the wet cotton and waxed paper was to prevent the drying out of the exposed surfaces. At intervals of one week after the time of inoculation certain limbs were removed, examined, and sections made to determine if there had been any growth of the mycelium into the living tissues. In most cases no trace of the mycelium could be found in the wood. In two or three branches there was a darkening of the surface exposed to the mycelium, and in the vessels the typical exudate which is produced by the mycelium, but so little mycelium was found in the ducts that the growth could not be identified, with certainty, as *Schizophyllum.* In only one branch was there an unmistakable infection. This was in a limb of a plum tree cut off three months after inoculation. The mycelium had penetrated to a maximum depth of 3 mm. and the infected area was about 4 cm. long and 1 cm. in width. Many hyphae were present in the vessels, and a few could be seen in the medullary ray cells. There was the characteristic darkened layer at the edge of the infection about 0.5 mm. thick. From the results of previous investigations and these experiments it is evident that the living woody tissues can be penetrated and killed by the mycelium of *Schizophyllum,* but that this process takes place slowly and with difficulty.

6. METHODS OF INFECTION UNDER NATURAL CONDITIONS

There have been many expressions of opinion in published papers concerning the manner in which living trees become infected with the mycelium of *Schizophyllum*. Infection takes place in three more or less distinct ways: (1) by entering through surfaces exposed by mechanical injury, (2) by attacking parts of trees weakened through certain physiological causes, and (3) by gaining admission through tissues first injured or killed by other organisms.

As regards mechanical injury, in Stevens and Hall (1910) it is stated that "apparently this disease starts in roots injured by tools during cultivation." Professor Horne of the University of California has observed an infection beneath an apple tree graft (fig. 1, pl. 58) that had not been properly sealed with wax. An infection at a crotch split in a peach tree (fig. 2, pl. 58) was reported by A. F. Camp, a student in the University of California. Any woody part exposed by injury forms a possible place of entrance for the fungus.

Weakening of the trees by excess water, or lack of proper drainage, was decided by Guegen (1901) to be a contributory cause of infection in horse chestnut trees. Stone (1910) found that sun scald and scorch of maple trees was followed by *Schizophyllum* and other fungi. The writer has seen the sunburned parts of California Bay trees covered with sporophores. It is evident that trees weakened by certain physiological agents fall prey to this fungus, and probably any loss of vitality on the part of the tree makes it susceptible to the attacks of *Schizophyllum*.

Wilson (1912) found that the sporophores issued through the burrows made by the shot hole borer (*Xyleborus dispar* Fabricus). Griffin (1911) stated that cherry trees weakened by bacterial gummosis are frequently attacked and killed by *Schizophyllum commune*.

No evidence has been brought forward in available literature to show that *Schizophyllum* is able to infect healthy trees, or those not injured or weakened in some way. It seems likely that infection can be prevented by using care in cultivation, by painting wounds made in pruning, by preventing crotch splitting, by protecting the trees from sunburning, and by keeping them free from other diseases.

7. ASSOCIATION WITH OTHER WOOD DECAY FUNGI

Fulton (1912) found that in an apple collar rot which he described *Schizophyllum commune* was present along with two other organisms.

Stone (1910) found in sun scald and scorch of maples that it was followed first by a canker fungus (*Nectria cinnabarina*), and then by *Schizophyllum* and *Polystictus.*

In the case of the apple graft mentioned above, the writer took the branch, sawed it into sections, and placed some of the sections in a moist chamber. From the decayed area a mass of mycelium appeared which was not of *Schizophyllum,* but as it has not yet produced any fruit bodies it cannot be identified.

Observations show that the fruit bodies of *Schizophyllum* are produced in a comparatively short time after inoculation has taken place. I have noted several times in the field that this fungus is the first to appear upon uprooted trees. Later, sporophores of *Polystictus, Polyporus, Tremella, Hydnum,* and other fungi are produced. Most of the pieces of wood I have collected in the field, which have only sporophores of *Schizophyllum* upon them, when placed in moist chambers long enough will produce sporophores of *Hydnum* or *Polystictus,* or both, long after a great number of fresh *Schizophyllum* fruit bodies have been formed. Since the hyphae of these other fungi were in the wood along with that of *Schizophyllum,* it is apparent that the latter fungus develops sporophores in a much shorter time than the others present. *Schizophyllum,* forming fruit bodies first upon a diseased tree, is naturally accused of being the parasite causing the damage. The writer believes that much or even most of the injury to trees attributed to this fungus is actually caused by the fungi so often associated with it, such as *Polystictus versicolor,* which is beyond doubt a parasite.[2]

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[2] Proof of the parasitism of *P. versicolor* was given by W. W. Thomas in 1916 at the University of California in a thesis submitted for a Master's degree. Mr. Thomas inoculated living trees with positive results as regards infection.

VI. SUMMARY AND CONCLUSION

In summarizing the morphology and development of *Schizophyllum* it may be said that:

1. The sporophores vary greatly as to form and shape.

2. The segments of the mycelium and sporophores and spores are regularly binucleate.

3. The fungus develops its sporophores as does no other member of the Hymenomycetes so far studied, the hymenium primordium arising in an apical cavity.

4. The "gills" arise upon the surface of an apical depression due to tensions set up by unequal rates of growth.

5. The "lamellae" are such by analogy only, being the edges of smooth hymenial areas, and therefore *Schizophyllum* belongs in the family Thellephoraceae.

As regards the economic aspects of *Schizophyllum*, it has been shown that:

1. Members of this genus are found throughout the tropical and temperate zones of the world.

2. They live upon a great number of woody plants, both in the Dicotyledonae, Monocotyledonae, and Gymnospermae.

3. The fungus possesses unusual vitality.

4. The mycelium is found only in small amount in infected wood.

5. It can grow upon fresh wood, and, under very favorable conditions, living wood.

6. Natural infection takes place through some injured or weakened part of the tree.

7. The fungus is usually associated with other parasitic fungi, which probably do most of the damage attributed to *Schizophyllum*, but escape attention due to the longer time necessary for them to produce fruit bodies.

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EXPLANATION OF PLATES

PLATE 51

Fig. 1. Group of sporophores in a dry condition, viewed from the lower side. 2 diameters.

Fig. 2. Group of sporophores in a moist condition, as seen from below. Some of the smaller specimens at the base of the group have been cut away. 1½ diameters.

1

2

PLATE 52

Fig. 1. Form of sporophores growing upon an under surface. *a*, side view of fruit bodies in position. *b*, the hymenium of a typical fruit body viewed from below, showing the gill plates radiating outward from a region near the center of the hymenium. ½ natural size.

Fig. 2. Form of fruit bodies growing upon a vertical surface. *a*, three sporophores in position. *b*, arrangement of the lamellar plates in a sporophore grown upon a vertical substratum. ½ natural size.

Fig. 3. Form of fruit bodies growing on an upper surface. *a*, position assumed by sporophores upon the upper surface of a limb. *b*, typical arrangement of the lamellar plates. ½ natural size.

Figs. 4–15. Views of young actively growing fruit bodies from the under side to show the origin and placement of the lamellar plates or ridges. All 5 diameters. Fig. 4, a sporophore with a smooth hymenium primordium just prior to the formation of lamellar ridges. Fig. 5, a fruit body with a single lamellar ridge. Fig. 6, a single lamellar ridge with the sides so far separated by sterile hyphae as to become merely edges of the hymenium primordium. Fig. 7, a specimen with four newly formed lamellar ridges. Figs. 8–14, six sporophores with some isolated ridges and some extending to the edge of the pileus. Fig. 15, a lateral sporophore with the lamellar ridges widening into sterile areas towards the base.

Fig. 16. Sporophore of *Cyphella Urbani*. 3 diameters. (After Engler and Prantl.)

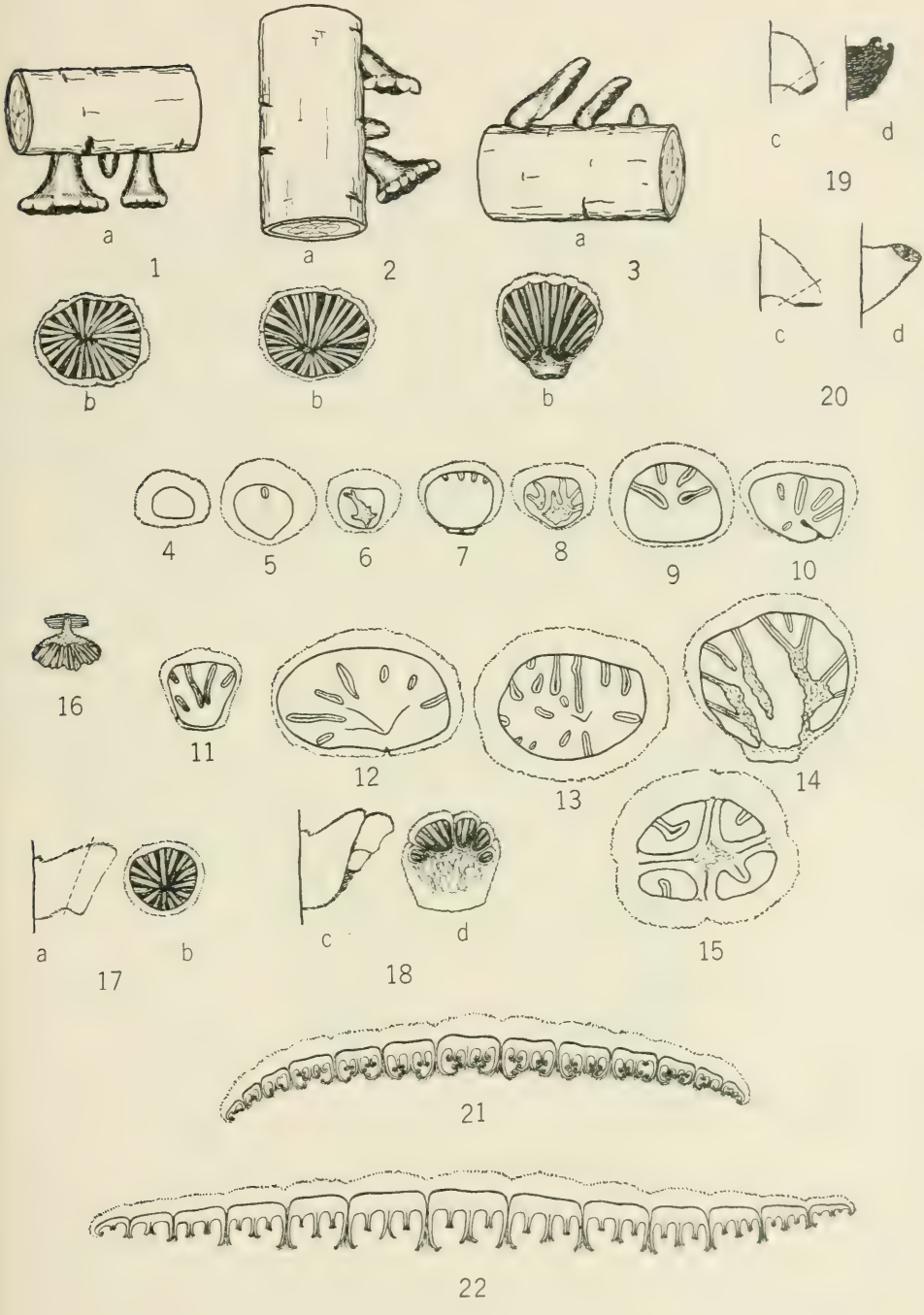
Figs. 17–18. Regeneration in position. *a*, a small sporophore showing with a broken line where the hymenophore was removed. *b*, face view of the hymenophore removed. 18*c*, side view of the sporophore after seven days. *d*, face view of the same, showing five small sporophores formed upon the cut end of the old stipe. All 1½ diameters.

Fig. 19. Regeneration inverted. *c*, a small fruit body showing where the end was cut away. *d*, a median section of the same thirty days later. Only one pair of lamellar plates was formed. 1½ diameters.

Fig. 20. Regeneration inverted. *c*, a small sporophore showing where the end was removed. *d*, the same a week after the apex had been cut away, showing three very small sporophores formed upon the cut end of the inverted stipe. These developed no further. 1½ diameters.

Fig. 21. A transverse section through a sporophore when in a dry state, showing the revolute lamellar plates, and their arrangement. 5 diameters.

Fig. 22. A transverse section through the same sporophore represented in fig. 21, but drawn while the sporophore was in a moist condition. 5 diameters.


a
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12
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14
a
b
17
c
d
18
15
21
22

PLATE 53

A sporophore in a semi-moist condition, as seen from below. The hymenium is shown to be divided into four areas, three of which are much smaller than the fourth. Several newly formed isolated pairs of lamellar plates can be seen, as well as three very small ridges near the center of the hymenophore which arose in an early development stage but remained isolated. 10 diameters.

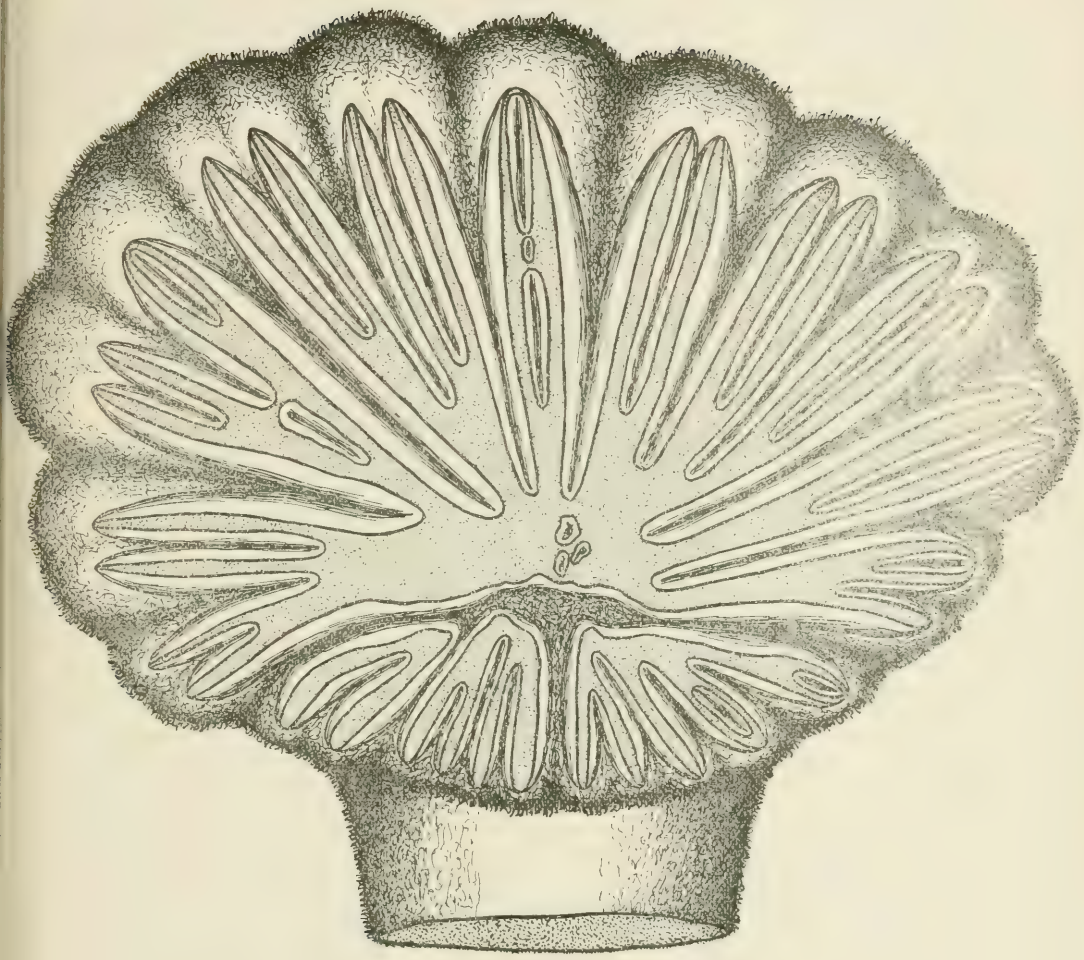

PLATE 54

Fig. 1. Part of a typical vegetative hypha to show the structural characters. Clamp connections are shown at each septum. The nuclei are near the center of each cell. 1500 diameters.

Fig. 2. Portion of a vegetative hypha covered with lateral projections. 1500 diameters.

Fig. 3. Hyphae which form the hairy covering of the pileus. They are usually unicellular, the nuclei being near the base of the cell. In this drawing a portion of each cell 1.4 mm. long was left out. This would represent a distance of about 210 cm. on the drawing paper. 1500 diameters.

Fig. 4. Portion of a longitudinal section through the flesh of a very young sporophore to show the hyphal structure. 1500 diameters.

Fig. 5. Same as in fig. 4, except that the section was taken from an old sporophore. . 1500 diameters.

Fig. 6. Portion of the hymenium, showing one mature and one immature basidium. 1500 diameters.

Fig. 7. Six typical spores, stained in safranin and gentian violet to show the nuclei. 2500 diameters.

Fig. 8. Germinating spores in various stages of development after being in distilled water for 48 hours. Stained in safranin. 1500 diameters.

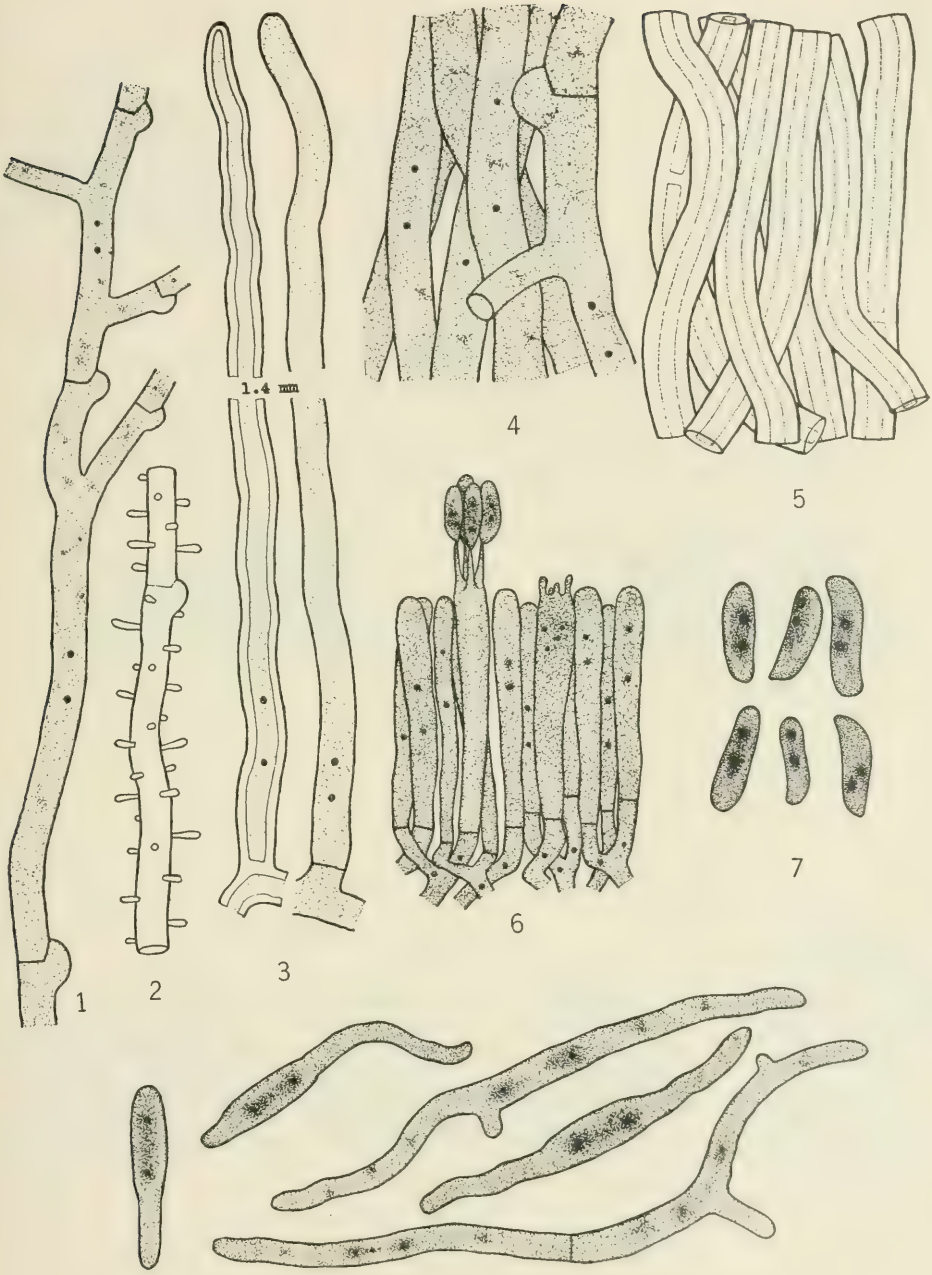
1.4 mm
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PLATE 55

Fig. 1. Longitudinal median section through a young fruit body which is practically undifferentiated. There is a region near the apex which stains more deeply and is the seat of later developments. 25 diameters.

Fig. 2. Similar to fig. 1, but a later stage, showing the first appearance of the apical cavity. 25 diameters.

Fig. 3. The apical cavity is still further developed. 25 diameters.

Fig. 4. Beginning of the palisade layer. 25 diameters.

Fig. 5. Further development of the palisade layer. 25 diameters.

Fig. 6. Maximum growth of the palisade layer in a plane surface. 25 diameters.

Fig. 7. The palisade layer (hymenium primordium) produced into a concave surface by the outward growth of the edges of the pileus. 25 diameters.

Fig. 8. Median longitudinal section through a small sporophore formed upon the cut end of a stipe. 18 diameters.

1

2

3

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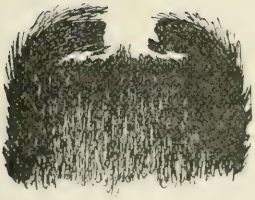
5



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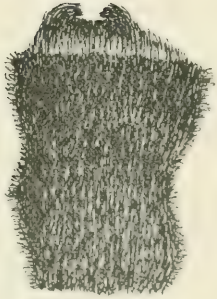


8

PLATE 56

Fig. 1. A piece of wood removed from the surface of an *Umbellularia* log, showing a number of very small sporophores in the earliest stage of development. Surface and side views. 2½ diameters.

Fig. 2. Shapes assumed by very young undifferentiated fruit bodies. 2½ diameters.

Fig. 3. A group of young fruit bodies in position upon a piece of *Umbellularia* bark. Five of the specimens are in the "apical cavity" stage, one is still undifferentiated, and another (at the extreme right) has already developed lamellar plates. 3½ diameters.

Fig. 4. Tangential section of *Acacia* wood to show the mycelium of *Schizophyllum commune* in a duct. About 125 diameters.

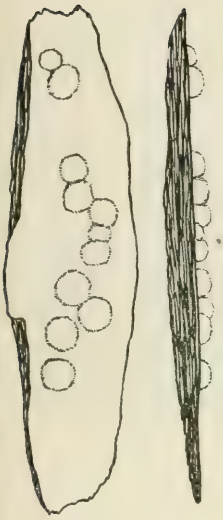
Fig. 5. Radial section of *Umbellularia* wood to show the hyphae of *Schizophyllum* in the ducts. About 125 diameters.

Fig. 6. Splitting of the palisade layer previous to the formation of a lamellar ridge. 250 diameters.

Fig. 7. Outward growth of the palisade layer at the sides of a split. 250 diameters.

Fig. 8. Loosening and outward growth of the elements of the palisade layer to form a lamellar ridge. 250 diameters.

Fig. 9. Cross-section of the palisade layer to show a very early stage in the origin of a lamellar ridge. 250 diameters.



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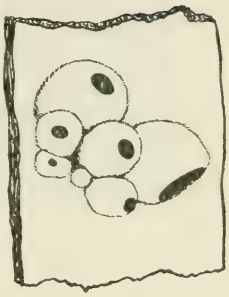

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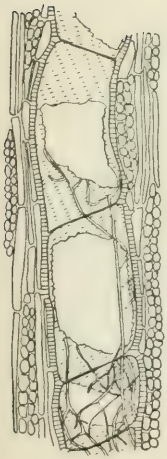

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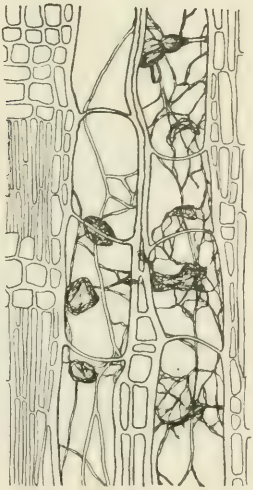

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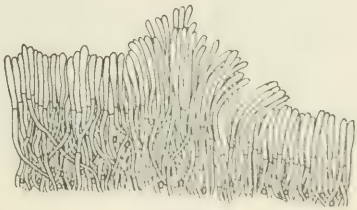

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PLATE 57

Fig. 1. A transverse section across a lamellar ridge in a very early stage of development. 448 diameters.

Fig. 2. A cross-section through a lamellar ridge divided down in the middle to form two small lamellar plates. 448 diameters.

Fig. 3. Another lamellar ridge in a stage of development similar to that shown in fig. 2. 448 diameters.

Fig. 4. A lamellar ridge whose halves are split apart deeply into the pileus flesh. 448 diameters.

1

2

3

4

PLATE 58

Fig. 1. Sections of apple limbs with the wood rotted by fungi penetrating through an improperly sealed graft. Sporophores of *Schizophyllum* appeared upon the bark of the tree beneath the graft about a year after the grafting was done. See the text for further explanation. ½ natural size.

Fig. 2. Sporophores of *Schizophyllum commune* in a dry condition upon the bark of a living peach tree at the side of a crotch split. The lower end of the split can be seen on the right side of the trunk. ½ natural size.

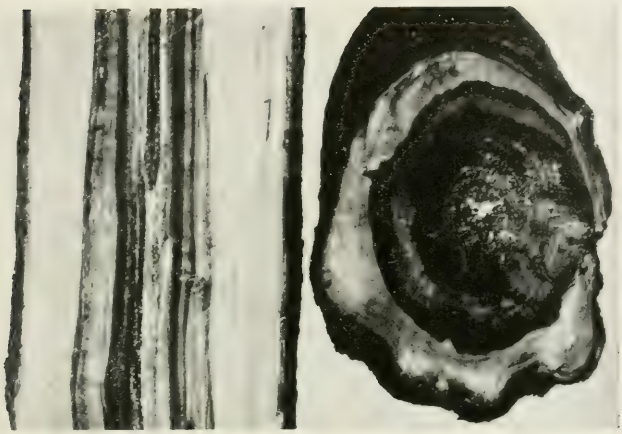

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PLATE 59

Fig. 1. A median longitudinal section through a very small undifferentiated fruit body. See fig. 1, pl. 54. 55 diameters.

Fig. 2. A median longitudinal section of a sporophore showing the breaking in of the apical cavity. 55 diameters.

Fig. 3. Photomicrograph of the section drawn in fig. 6, pl. 54. 55 diameters.

Fig. 4. A median longitudinal section through a fruit body with the apical cavity fully developed. 55 diameters.

1

3

2

4

PLATE 60

Fig. 1. A widened lamellar ridge in cross-section, showing the sterile area between the edges of the hymenium. 75 diameters.

Fig. 2. A sporophore developed from a single lobe of a mutilated inverted specimen. For a further description see the text. 2 diameters.

Fig. 3. A median longitudinal section through a regenerated sporophore. See text for further explanation. 75 diameters.

1

2

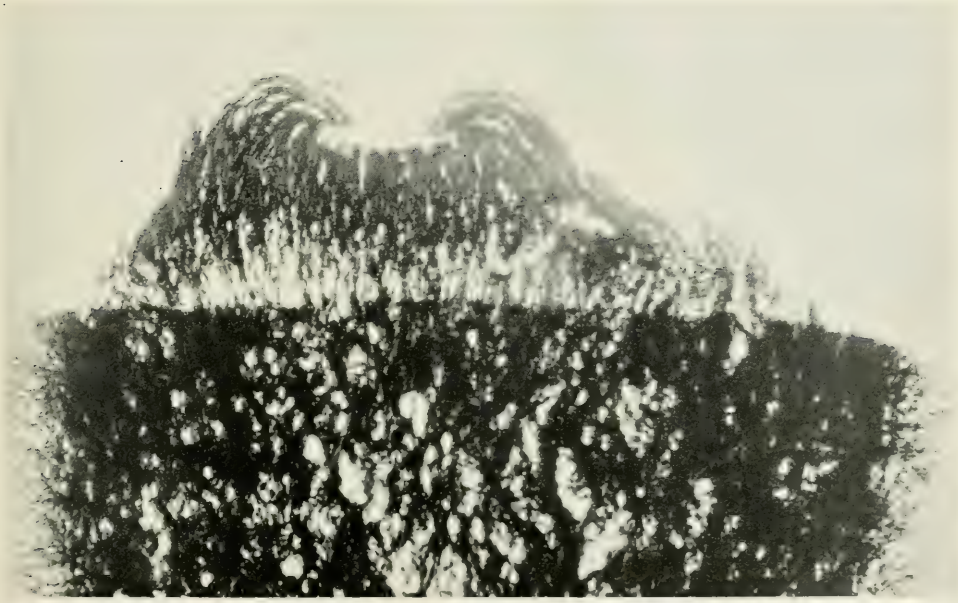

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PLATE 61

A radial section through *Umbellularia* wood with the hyphae of *Schizophyllum commune* in the tracheae. 350 diameters.

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ERRATA

Page 277, line 14 from bottom. *For* Guiterrezia *read* Gutierrezia.

Page 443, line 6 from bottom. *Read:* "cystocarpiis et spermatangiis in hieme, cum tetrasporangiis in hieme et vere lecta."

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A RUBBER PLANT SURVEY OF WESTERN NORTH AMERICA

BY
HARVEY MONROE HALL
AND
THOMAS HARPER GOODSPEED

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II. ON THE CALIFORNIAN "DELESSERIA QUERCIFOLIA"

BY

CARL SKOTTSBERG

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IVAN MURRAY JOHNSTON

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I

BY
WILLIAM ALBERT SETCHELL
AND
NATHANIEL LYON GARDNER

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WILLIAM ALBERT SETCHELL
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BY

THOMAS HARPER GOODSPEED

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II. THE NATURE AND OCCURRENCE OF UNDEVELOPED FLOWERS

BY
THOMAS HARPER GOODSPEED AND ROBERT PERCY BRANDT

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